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Niche modelling suggests low feasibility of assisted gene flow for a Neogene relict tree, *Castanea sativa* Mill.

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Abstract: As many tree species populations are being degraded by climate change, adaptive conservation, and forest management, such as assisted gene flow (AGF), can provide the genetic variation needed to adapt to climate change. The core of this strategy is to assist the adaptation process in populations at risk of climate maladaptation by introducing individuals with beneficial alleles to cope with expected climate changes. *Castanea sativa* Mill. (sweet chestnut) is an essential component of natural forests in the Mediterranean and Caucasian regions, with a long history of cultivation. Current climate change may seriously threaten the long-term persistence of the species, particularly in the Caucasus region, where the largest range reductions are predicted. Here, we used Species Distribution Models (SDMs) to assess the feasibility of AGF in European and Caucasian populations of *Castanea sativa*. Bioclimatic variables for present (1981–2010) and future (2071–2100) conditions were obtained from the CHELSA climate database. The final models of future species ranges were averaged across three climate models (IPSL-CM6A-LR, MPI-ESM1-2-HR and UKESM1-0-L) and three climate change scenarios – SSP1-2.6, SSP3-7.0 and SSP5-8.5. There are marked differences in the climatic niches of the Iberian, Alpine-Apennine, Balkan, and Caucasian populations, with significant implications for AGF. The most suitable European areas for the Caucasian populations were found only in the Adriatic region. The Iberian populations were not compatible with the predicted future climate in the Caucasus in any of the scenarios tested. Suitable areas for Alpine-Apennine populations within the AGF strategy were predicted in the Colchic lowlands, the eastern Pontic mountains and the Hyrcanian forests in the SSP1-2.6 and SSP3-7.0 climate change scenarios. In contrast, the Balkan populations would be compatible at most with the western Pontic mountains and, to a lesser extent, with the Hyrcanian forests. According to the most damaging climate scenario SSP5-8.5, the potential of AGF in the Caucasus with Alpine-Apennine and Balkan populations could be very limited. Our study showed limited applicability of AGF for *Castanea sativa* between the European and Caucasian populations due to low climate match. Genomic modelling is needed to fully assess the feasibility of this strategy in the species.

Keywords: climate change, Caucasus, sweet chestnut, range modelling, maladaptation, adaptive management

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Introduction

Species extinction is at the center of the debate on biodiversity loss. However, population loss is occurring at a faster rate than species loss and is likely to be a more important conservation problem globally (Urban, 2015; Briggs, 2017). Population decline threatens species with extinction because smaller populations are more susceptible to inbreeding and genetic drift, leading to loss of genetic diversity and impairment of evolution, including the adaptive process. The population declines already reported are severe (Briggs, 2017; Stanke et al., 2021). Many tree species are threatened with extinction due to anthropogenic factors such as deforestation, fragmentation, pollution, and land-use change (Rivers et al., 2019). Ongoing climate change is also one of the most severe threats to trees. For example, trees are increasingly reported to suffer from heat waves, which cause large-scale mortality of their populations (Allen et al., 2010; Buras et al., 2018; Senf et al., 2020). Furthermore, the distributional projections also predict significant losses of ranges (Dyderski et al., 2018; Illés & Móricz, 2022; Mauri et al., 2022).

Adaptation, migration, plastic response, or extinction are the possible outcomes for tree populations as a result of the ongoing global climate crisis (Aitken et al., 2008). During the Pleistocene and much of the Holocene, the response of tree populations to changing environments was sufficient to survive and evolve (de Lafontaine et al., 2018). However, the current pace of climate change appears to be too fast for many populations to track these changes, putting them at risk of maladaptation and extinction. As forests are reservoirs for biodiversity and are essential for providing ecological, economic, and societal benefits, it is of utmost importance to develop new strategies aiding the survival of trees locally, regionally, and globally (Lachmuth et al., 2023). Therefore, conservation and management strategies for species should focus even more on populations than on species, and include new approaches to climate change mitigation (Millar et al. 2007; Lefèvre et al., 2013; Gömöry et al., 2020; Kurz et al., 2023).

The paradigm of "local is the best" led to the use of local germplasm for conservation efforts and active management of forests (Prober et al., 2015; Myking et al., 2016). While the use of locally adapted seeds ensures endurance against environmental challenges by utilizing local adaptation, "local is the best" is questioned about being not fast enough to track the rapid climate change and resist disruption of the adaption of local populations (Konnert et al., 2015). At the population level, one of the climate change mitigation strategies to avoid maladaptation is the managed translocation of germplasm of individuals or populations to new areas. This idea has been translated into the concept of assisted migration (AM). In its broadest sense, it is defined as the deliberate translocation of individuals within or beyond the natural range of a species (Aitken & Witlock, 2013). For the most part, AM is discussed in the context of human-mediated expansion of the natural range of species, or the introduction of the target species into areas where it has not historically been recorded (McLachlan et al., 2007; Hewitt et al., 2011; Aitken & Witlock, 2013). In contrast, assisted gene flow (AGF) is methodologically embedded in the natural range and refers to the managed movement of individuals or gametes between populations within the natural range of a species (Aitken & Witlock, 2013).

Assisted gene flow is a strategy that is being considered as a potentially highly effective forest management and conservation option to address the current climate changes and related risks (Aitken & Bemmels, 2016; Aitken & Whitlock, 2013; Browne et al., 2019). The expected outcome is an increase in population fitness by introducing genotypes pre-adapted to new climates or increasing their frequency in the target populations. AGF aims therefore not only the prevention of extinction but mostly the improvement of the fitness of populations in the new climatic future, with long-term persistence as the ultimate goal. However, although AGF is considered as a management tool in mitigating the climate crisis, it is still controversial as it implies a risk of failures. Firstly, climate change is predicted with considerable uncertainty. Secondly, other factors than climate may drive the local adaptation (Wadgymar et al., 2015). Also, there are potentially harmful genetic consequences on AGF, such as outbreeding depression and disruption of the local adaptations to factors other than climate (e.g. photoperiod, soil etc.) which may decrease the fitness of targeted populations (Aitken & Whitlock, 2013). In case of adaptive hybridization, which may be a form of AGF between closely related species (e.g., *F. sylvatica* and *F. orientalis*; Kurz et al., 2023), the risk of genetic swamping and loss of local lineages through evolutionary replacement should be considered.

Castanea sativa Mill. (sweet chestnut) is a highly economically and ecologically important tree species distributed in the countries of the Mediterranean Basin, Central Europe, and West Asia - the Caucasus (Fig. 1; Conedera et al., 2004; Freitas et al., 2022; Aglietti et al., 2022). It is an iconic tree species in the Mediterranean countries, a pillar of their agroforestry (Freitas et al., 2021; Braga et al., 2023) and vital biocultural element of the region (Pollegioni et al., 2020). Being the Neogene relict, sweet chestnut contributes importantly to the natural evolutionary heritage of the European and West Asiatic flora. The species has been the subject of many studies in the European range, dealing with the evolutionary history of the species or the factors underlying the spatial distribution of genetic variability in the context of human cultivation and adaptation to climate change (e.g., Míguez-Soto et al., 2019; Pollegioni et al., 2020; Castellana et al., 2021). In contrast, few studies have examined Caucasian populations, despite the species' prominent role in the region's forest ecosystems. In the Western Caucasus, sweet chestnut forms pure stands, some of which still retain the character of past Neogene forests, and remains the key component of the forest vegetation of the mid-elevation belt (Nakhutsrishvili, 2013). The most comprehensive studies conducted in the Caucasus, which included 21 natural populations and covered the entire range, demonstrated the retaining of high genetic diversity in sweet chestnut and intensive gene flow, resulting in moderate genetic differentiation (Beridze et al., 2023a). Similar to initial studies (Mattioni et al., 2017), the Western Caucasus was identified as harbouring the highest genetic diversity (Beridze et al., 2023a). A reconstruction of the demographic history of the species revealed long-term genetic isolation between European-Caucasian gene pools since the mid-Pleistocene and concluded that conservation of diversity in the Caucasus is a high priority for species adaptation and future breeding programmes (Beridze et al., 2023b).

The natural history of the *C. sativa* in Europe is marked by domestication and cultivation dating back to the Neolithic period, but it was not until the Middle Ages that the species began to be planted and bred on a large scale (Conedera et al., 2004, 2016). Similarly to Euro-Mediterranean, in the Caucasian range, the species was appreciated as a valuable source of timber, fruits and honey but this isolated gene pool was much less affected by cultivation (Bobokashvili & Maghradze, 2009, Beridze et al., 2023a, b). In a result of the socio-economic changes in Europe since the 18th century and the mass dying off at the beginning of the 20th century due to novel and aggressive pests and diseases, the species has become less important for the European economy (Zlatanov et al., 2013; Condera et al., 2021). However, it recently gains increased attention as the potential tree of choice for forestry in new climatic conditions. Such suggestions came from studies indicating the adaptive responsiveness of the species to drought (Míguez-Soto et al., 2019; Castellana et al., 2021). Although the experimental studies carried out on young seedlings do suggest resistance to drought (Camisón et al., 2020), this effect does not need to be transferred to older ontogenetic stages and maintained in natural conditions. For example, in Spain, the productivity and survival of sweet chestnut is compromised by recent climate changes (Alcaide et al., 2019).

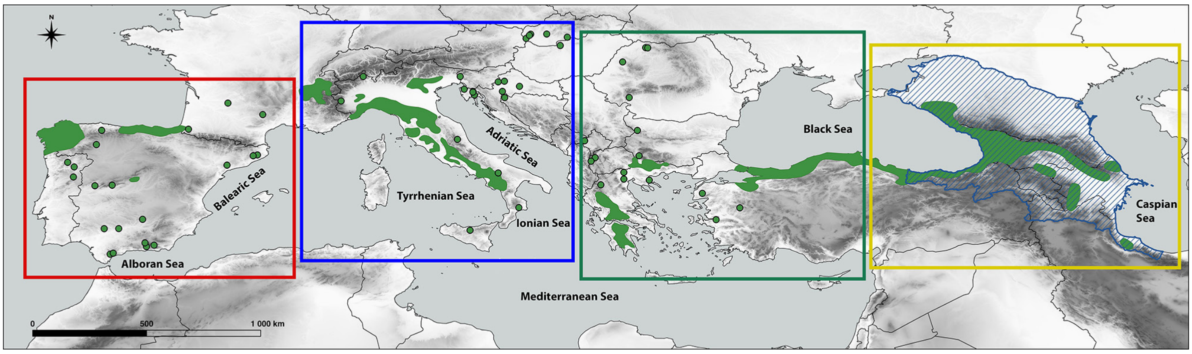

Fig. 1. Natural distribution of *Castanea sativa* in Europe and the Caucasus based on Caudullo et al. (2017), Poljak et al. (2017) and Castellana et al. (2021). The blue dashed area delineates the Caucasus ecoregion, dots refer to the isolated stands. Red-Iberian populations; blue-the Alpine-Apennine populations; green - the Balkan populations and yellow - the Caucasian populations

Species Distribution Models (SDMs) predict the future expansion of sweet chestnut into northern European areas but at the expense of some losses in the core range, in the southern European part (Mauri et al., 2022; Freitas et al., 2022). Other study suggests significant losses in the area suitable for the species' grow in the future in Europe (Castellana et al., 2021). The species is predicted to decline drastically in the Caucasian range because of climate change, with potential negative impacts on genetic resources. According to Beridze et al. (2023a), the eastern part of the species' natural range in the Caucasus may be lost due to climate change, resulting in a pronounced genetic impoverishment of this regional gene pool. Genetically informed conservation management to secure the species' genetic resources in the Caucasus has been outlined (Beridze et al., 2023a). A serious threats to *C. sativa* are pests and diseases that are intensified by climate change and decimate stands in Europe and the Caucasus, especially those with already reduced fitness due to abiotic stresses (Fernandes et al., 2022). A recent study challenges the perception of the species as a future-proof tree in Europe due to its low competitive ability, which requires silvicultural management to achieve desired productivity and wide distribution (Conedera et al., 2021). The low competitiveness of the species and limited potential of dispersal challenge the natural ability of sweet chestnut to expand northward, as projected by SDMs in response to the expected climate change. It therefore appears that the future of this valuable tree species in Europe and the Caucasus may be significantly dependent on human interventions and adaptive management tools, such as AGF.

Despite the static approaches to defining future ranges offered by SDMs, they can provide initial guidance for the conservation and management of tree populations and have been shown to provide information on potentially maladapted populations (Pecchi et al., 2019; Sękiewicz et al., 2020; Mauri et al., 2022; Mellert & Šeho, 2022; Alipour et al., 2023). Ideally, climate modelling combined with recognised local adaptation patterns should inform the design of AGF strategies and policies (e.g., Borrell et al., 2020). However, searching for loci involved in local adaptation is challenging because of the complex determinism of these traits (e.g., Bruxaux et al., 2023). Hence, despite their shortcomings, climatic models based on SDMs are one of the simplest tools for the initial predicting the global and local impacts of climate change on the future distribution of species (Mauri et al., 2022; Sękiewicz et al., 2022; Beridze et al., 2023a).

In this work, we investigated the possibility of using SDM to guide sweet chestnut management in future climates within the AGF approach. SDMs provide a relatively simple way to gain initial insights into the climatic compatibility between source and target populations, which is the baseline for this adaptive management. Using SDMs, we aimed to assess the climatic compatibility between the European and Caucasian gene pools of sweet chestnut and to identify the climatic factors underlying the possible outcome of such adaptive management in different climatic scenarios. The results of this work may benefit future sweet chestnut breeding and conservation programs in Europe and the Caucasus.

Materials and Methods

Species occurrence data

The data on the species' natural distribution was acquired from Caudullo et al. (2017), Janfaza et al. (2017) and Beridze et al. (2023a, b). In terms of distributional records, we choose the points locations inside the range polygon randomly. Closely located spots were automatically treated by the MaxEnt algorithm as one record. Due to the marked climatic differences, the European occurrence spots of the species were divided into three subsets representing the Iberian gene pool (western; 295 geospots), Apennine-Alpine gene pool (central; 487 geospots) and Balkan gene pool (eastern; 387 geospots) of the species (Fig. 1). The Caucasian range of the species was represented by 825 geospots (Beridze et al., 2023a, b). This number of records fulfil the requirements of building accurate species distribution models in MaxEnt (van Proosdij et al., 2016; Sarıkaya et al., 2022). The subdivision of the natural range of the sweet chestnut that has been adopted in this work is also justified by the schemes used in the international provenance trials (e.g., Maurer & Fernández-López, 2001). As a result, four simulations have been launched for mapping of the suitable areas for AGF management in sweet chestnut, including 1) the Caucasian populations for the European range, 2) the Iberian populations for the Caucasian region, 3) the Apennine-Alpine populations for the Caucasian region and 4) the Balkan populations for the Caucasian region.

MaxEnt simulations

We investigated the distribution of *C. sativa* using the maximum entropy algorithm implemented in MaxEnt 3.4.3 (Phillips et al., 2006) and used the bioclimatic variables available on the CHELSA 1.2 (Climatologies at high resolution for the earth's land surface areas; Karger et al., 2017; Karger et al., 2021) for current (1981–2010) and future (2071–2100) climatic conditions at 0.5' resolution. The main advantage of CHELSA database is that the precipitation algorithm incorporates orographic predictors, including wind fields, valley exposure and boundary layer height, with subsequent bias correction. In result, it may outperform widely used WORLDCLIM database (Bobrowki et al., 2021), especially in complex landscapes such as mountainous areas. We obtained 19 bioclimatic variables (bio1–19; Table 1) using the latest Coupled Model Intercomparison Project (CMIP6) (Eyring et al., 2016; Meinshausen et al., 2020) for three future Shared Socioeconomic Pathways (SSPs) scenarios: SSP1-2.6, SSP3-7.0, and SSP5-8.5 (IPCC/CMIP6). Scenario SSP1-2.6, with a radiative forcing of 2.6 W/m^2 by 2100, describes the optimistic conditions simulating the targeted 2 °C increase in global mean temperature and an atmospheric CO_2 concentration of 393 ppm, assuming mitigation actions are taken. Next, the SSP3-7.0 scenario, which assumes a radiative forcing of 7 W/m^2 by 2100 with a CO_2 concentration of 867 ppm, represents the upper-middle part of the full range of scenarios and predicts a global mean temperature increase of up to 3.6 °C. Finally, the most pessimistic scenario, SSP5-8.5, assumes a development based entirely on fossil fuels, leading to an atmospheric CO_2 concentration of 1135 ppm, with a radiative forcing of 8.5 W/m^2 and a global mean temperature of 4.4 °C by 2100 (Meinshausen et al., 2020). To obtain reliable and unbiased estimates, three global circulation models out of five currently available on CHELSA were used: IPSL-CM6A-LR, MPI-ESM1-2-HR, and UKESM1-0-LL. These climatic models were of highest recommendation to use in modelling (Karger et al., 2021) and were chosen considering the Inter-Sectoral Impact Model Intercomparison Project (ISIMIP3b) protocol suggestions (Karger et al., 2021; https://www.isimip.org/protocol/3/). All downloaded rasters were standardized with QGIS 3.16.3 'Białowieża' (QGIS Development Team, 2022).

Table 1. Description of predictive bioclimatic variables available in CHELSA database of climatologies. Bioclimatic variables used in the final modelling in this study are shown in bold

Code	Name	Unit
bio1	**mean annual air temperature**	**°C**
bio2	mean diurnal air temperature range	°C
bio3	**isothermality**	**°C**
bio4	**temperature seasonality**	**°C/100**
bio5	**mean daily maximum air temperature of the warmest month**	**°C**
bio6	mean daily minimum air temperature of the coldest month	°C
bio7	annual range of air temperature	°C
bio8	mean daily mean air temperatures of the wettest quarter	°C
bio9	**mean daily mean air temperatures of the driest quarter**	**°C**
bio10	mean daily mean air temperatures of the warmest quarter	°C
bio11	mean daily mean air temperatures of the coldest quarter	°C
bio12	annual precipitation amount	kg m^{-2}
bio13	**precipitation amount of the wettest month**	**kg m^{-2}**
bio14	**precipitation amount of the driest month**	**kg m^{-2}**
bio15	precipitation seasonality	kg m^{-2}
bio16	mean monthly precipitation amount of the wettest quarter	kg m^{-2}
bio17	mean monthly precipitation amount of the driest quarter	kg m^{-2}
bio18	mean monthly precipitation amount of the warmest quarter	kg m^{-2}
bio19	**mean monthly precipitation amount of the coldest quarter**	**kg m^{-2}**

First, to deal with multicollinearity we performed autocorrelation analyses for the current period (1981–2010) bioclimatic variables using *layerStats* function based on Pearson's correlation analysis (package *raster* 3.5–15; Hijmans et al., 2015), and the multicollinearity cutoff=0.9 was used to select the subset of non-collinear variables. Next, the *vif* function implemented in the *usdm* R package (Naimi et al., 2014) was applied to select the final set of variables used in modelling. As a result, five temperature and three precipitation-related predictive bioclimatic variables were used in the final simulations (Table 1). Next, using Caucasian geospots and the current period bioclimatic variables, the MaxEnt model was trained to project calibrated algorithms for each future climatic scenario (2071–2100) and studied climatic models in the European range. In the reverse analysis, subregional European geospots (Iberian, Apennine-Alpine and Balkan) were used to predict suitable future areas in the Caucasus ecoregion. MaxEnt was run with a "random seed" option and 20% of input data was used for model testing and 100 bootstrap replications were chosen with maximum iterations of 10^4 and output was set as logistic. Model accuracy was evaluated using the area under the receiver operating curve (AUC) values of the receiver operating curve (ROC) as a threshold-independent evaluation metric (Mas et al., 2013). The AUC is based on the ROC curve, the shape of which depends on the sensitivity of the model (the ratio of true positives to the sum of true positives and false negatives) and its specificity (the ratio of true negatives to the sum of true negatives and false positives). The AUC is the value of the area under the ROC curve, which determines how well the model can discriminate between classes. A perfect model has an AUC close to 1. The AUC value of 0.5 indicates that the model is close to random, while a value of 0 indicates the inverse of the true observations (predicts a negative class as a positive class and vice versa). The area of distribution (in km^2) was computed in QGIS using the *$area* function for two thresholds ≥10% and ≥50% of habitat suitability for sweet chestnut.

Results

Simulations validation

The scores of AUC values were high (>0.95), indicating good fitness of the models (Table 2). The lowest support for model performance was obtained in simulations of the suitability areas for the Apennine-Alpine populations in the Caucasus (0.957, 0.958 and 0.986 for SSP126, SSP370 and SSP585, respectively) and the highest in simulations of the suitability areas for Iberian populations in the Caucasus (0.983, 0.985 and 0.983 for SSP1-2.6, SSP3-7.0 and SSP5-8.5, respectively, Table 2).

The contribution of precipitation- and temperature-derived variables varied largely depending on the scenario (Table 2). The Caucasian populations were the most divergent - bio14 (precipitation of driest month) was a single and the most important variable, reaching nearly 60% of contribution in the simulations, while all remaining variables were of much less importance (Table 2). The Iberian populations are also outstanding because two other climatic variables - bio4 (temperature seasonality >40%) and bio19 (precipitation of the coldest quarter, 37–40%) were the only two strongest predictors. For the Balkan and Apennine-Alpine populations, precipitation-related bioclimatic variables were the most important factors. Precipitation of the coldest quarter (bio19) had a contribution of 27–28% for the Balkan range, while for the Apennine-Alpine populations precipitation of the driest month (bio14) was more significant with a contribution of 28–29%. Temperature seasonality (bio4) was equally important in both regions with a contribution ca. 18%.

The probability of *C. sativa* occurrence in the Caucasus increased with high values of the precipitation-derived variables, which also have much wider ranges compared to the Balkan, Iberian, and Apennine-Alpine ranges of the species (Fig. 2). Thermal niche of sweet chestnut in the Caucasus differs significantly from the European range, especially in terms of bio9 (mean temperature of the driest quarter). Accordingly, the highest probability of the species occurrence coincides with the temperatures below zero for bio9 while the species requires a temperature of at least 16 °C in the European range during the driest quarter (Fig. 2). In comparison to the European regions, sweet chestnut in the Caucasus also experiences higher temperature seasonality and the lower annual mean temperature (Table 3). In the driest month, the mean precipitation in the Caucasian range of the species is higher than in Europe (on average 74.1 mm). For example, in areas occupied by sweet chestnut in the Balkans, the mean precipitation of the driest month is only 35.9 mm. However, while the driest months

Table 2. Model performance expressed by area under receiver operating curve (AUC) and contribution of the most important bioclimatic variables to the SDMs projections for tested gene pools of *Castanea sativa*. Values are averaged across three global circulation models used

Scenario	AUC	bio1	bio3	bio4	bio5	bio9	bio13	bio14	bio19
Caucasus									
SSP1-2.6	0.981	14.40	10.60	1.00	1.30	0.80	1.90	58.60	5.40
SSP3-7.0	0.980	14.50	10.20	1.00	1.10	0.70	1.90	59.50	5.20
SSP5-8.5	0.980	15.20	10.30	1.10	0.90	0.70	1.90	58.80	5.00
Balkan									
SSP1-2.6	0.980	1.00	1.10	18.77	1.20	19.90	1.77	16.33	27.47
SSP3-7.0									
SSP5-8.5	0.980	0.97	0.93	18.23	1.20	17.27	1.83	15.70	27.23
Alpine-Apennine									
SSP1-2.6	0.957	0.77	1.40	18.60	2.70	6.20	22.67	28.40	8.07
SSP3-7.0	0.958	0.77	1.37	18.37	2.93	6.27	22.90	28.40	8.03
SSP5-8.5	0.956	0.93	1.47	18.10	2.47	6.63	21.53	29.13	7.43
Iberian									
SSP1-2.6	0.983	0.70	3.50	42.23	0.87	0.70	1.17	6.10	38.70
SSP3-7.0	0.985	0.73	3.30	40.80	0.90	0.73	1.20	5.97	40.13
SSP5-8.5	0.983	0.87	3.10	44.53	0.87	0.80	1.37	5.33	37.27

Table 3. Average values of the most important bioclimatic variables in the SDMs projections of *Castanea sativa* in different regions

	bio1	bio3	bio4	bio9	bio13	bio14	bio19
Caucasus	8.95	29.04	757.35	8.54	163.08	74.14	319.51
Alpine-Apennine	11.29	32.22	648.93	14.31	143.26	50.24	272.56
Balkan	12.23	32.28	669.29	20.09	135.82	35.09	328.53
Iberian	12.45	38.58	403.71	17.69	209.23	47.19	498.20

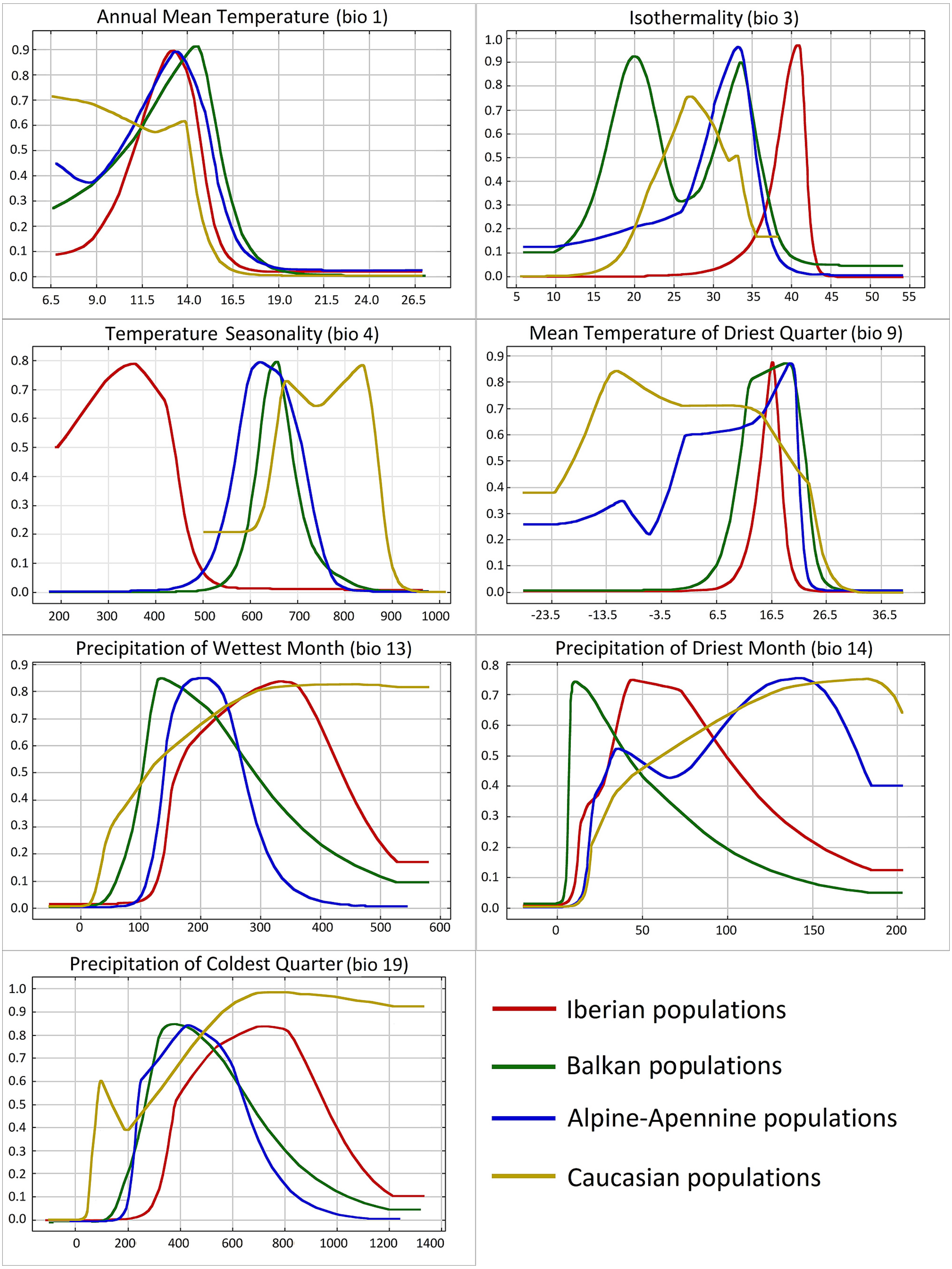

Fig. 2. Bioclimatic variables gained from CHELSA with the highest contribution in SDMs projections showing variable current climatic requirements of *Castanea sativa* populations, including the Iberian, Balkan, Alpine-Apennine, and Caucasian regions

in the Caucasus fall into the winter, it is the opposite for the European regions for which the summer period is the driest. The most divergent in terms of the occupied climatic niche, especially precipitation, are sweet chestnut populations from the Iberian Peninsula. Those populations experience the highest precipitation in the coldest quarter compared to the other regions of Europe and the Caucasus (Table 3).

Climate-based areas suggested for AGF

The climate-based future suitable areas for the sweet chestnut from the Caucasus at SSP1-2.6 climate change scenario encompasses central and Southern Europe (Fig. 3) and amounts to a total of 755,927 km^2. The most preferable areas for AGF would be restricted to the north-eastern shores of the Adriatic Sea (Italy-Slovenia-Croatia) where the suitability was predicted to reach >70%. Additionally, high probability habitats (suitability ca. 50%) were also projected in two disjunct pockets in Italian Alps and Jura mountains (Fig. 3, A). Under the SSP3-7.0 scenario, SDM predicts roughly a similar geographic area suitable for the Caucasian populations but with a reduction of the areas having suitability ≥50%. The most damaging climatic change scenario of SSP5-8.5, is likely to drastically limit theoretical suitable areas for the Caucasian populations of sweet chestnut in Europe. Specifically, the overall distribution considered with at least 10% suitability is 45% less, and the highly suitable areas considered with at least 50% suitability are ca. 86% less compared to the SSP1-2.6 optimistic climate change scenario (Fig. 3C).

In general, the future climate in the Caucasus is unlikely to provide climatically suitable habitats for the European populations of sweet chestnut over a wide area (Figs 4–6). Additionally, there is strong variability between populations and scenarios. Among the tested projects of AGF, the Iberian populations are predicted to be the worst adapted to the future climate in the Caucasus, while the Alpine-Apennine gene pool seems to be much better adapted. Also, the usefulness of the Balkan gene pool for AFG in the Caucasus would be moderate under SSP1-2.6, but in the warmer scenario of SSP3-7.0 these populations could be better suited than the Alpine-Apennine populations. However, in the case of both gene pools, the eastern Pontic mountains and the areas of the Hyrcanian forests are predicted to be the most suitable in comparison to the South Caucasus, which includes the territories of Georgia and Azerbaijan. The exception is a limited area in the western parts of the region - the Colchic lowlands and Adjara. Furthermore, in the SSP1-2.6 scenario, the model predicted future suitable climatic conditions for the Balkan gene pool in southern Türkiye, where chestnut is currently absent.

Discussion

Climatic incompatibility between European and Caucasian ranges

The close evolutionary relationship between Europe and the Caucasus is evidenced by the sharing of many plant genera, species, or sister taxa between the two regions (Tarkhnishvili, 2014; Manafzadeh et al., 2017). In addition to *C. sativa*, economically important forest tree species in the Caucasus include *Pinus sylvestris* subsp. *hamata* Steven, *Abies nordmanniana* (Steven) Spach, *Picea orientalis* (L.) Carr., *Alnus glutinosa* subsp. *barbata* (C.A. Mey.) Yalt., *Carpinus betullus* L., *C. orientalis* Mill., *Quercus petraea* (Matt.) Lieb., or species belonging to *Tilia* L. and *Acer* L. Long periods of genetic isolation between Euro-Siberian, Mediterranean, and Caucasian populations have resulted in genetic differentiation, which is likely to have been driven by adaptive divergence. As a result, phylogenetically close taxa now grow in ecologically very different habitats in Europe and the Caucasus (Dering et al., 2021; Sękiewicz et al., 2022). Therefore, the Caucasian populations of sister or closely related species currently found in Europe appear to be perfect candidates for AGF in the new climatic conditions (e.g., Kurz et al., 2023).

Recently, studies investigating AFG for *Fagus sylvatica* with the subspecies *F. sylvatica* subsp. *orientalis* distributed in the Caucasus region conducted with SDMs suggest the potential genetic gains of such management strategy (Mellert & Šeho, 2022; Kurz et al., 2023). In contrast, our SDMs-based analysis predicted a limited application of AGF in the European populations of *C. sativa* with the Caucasian populations. We estimated that the highly suitable areas for the Caucasian populations cover only about 30% of the current theoretical natural distribution of the species in Europe. According to our autecological analysis, the Caucasian populations grow in a much wetter climate, with higher rainfall during the driest periods, which likely explain the general mismatch between ranges. Given the relatively stable future distribution of *C. sativa* across the European range predicted by SDMs (Mauri et al., 2022) and the high genecological variability of the species (e.g., Mattioni et al., 2017; Fernández-López et al., 2021), it is likely that, if required, AGF in the European range could be based solely on the diverse European gene pool. On the contrary, drastic losses of the species are predicted in the Caucasian range by SDMs (Beridze et al., 2023b), and AGF for this region appears to be very limited with the different European gene pools tested in this study (Iberian, Alpine-Apennine, and Balkan). In fact, none of the European gene pools match the current core range of sweet chestnut in the South Caucasus, and the Iberian populations are

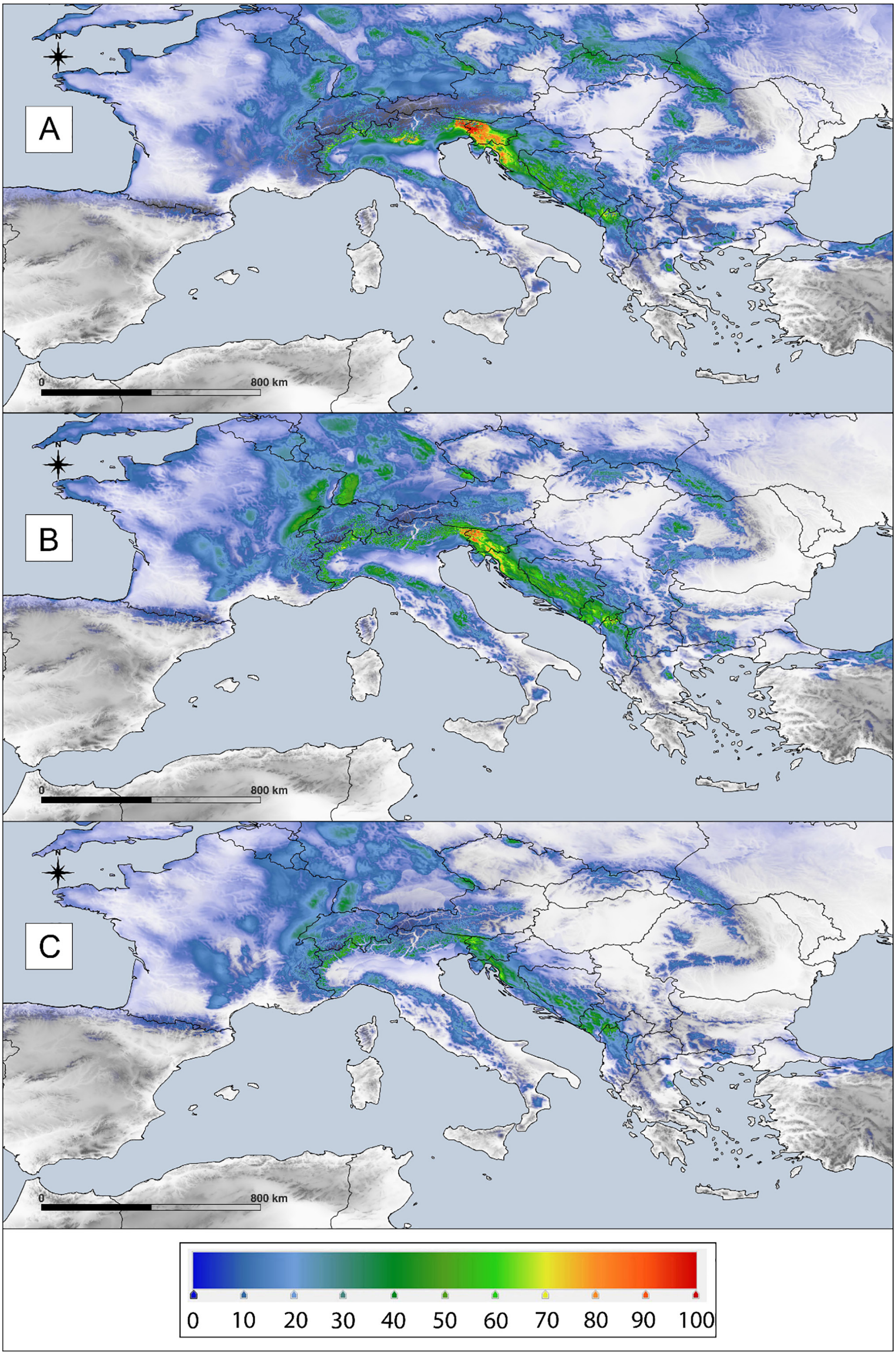

Fig. 3. Maps of the theoretical suitable areas in Europe for the Caucasian populations of *Castanea sativa* simulated using Maxent, representing theoretical ranges in 1971–2100 for three climatic scenarios employed: A – SSP1-2.6, B – SSP3-7.0, and C – SSP5-8.5; habitat suitability chart in percentages

completely mismatched (Figs 4–6). The most suitable areas for the European populations to grow in the Caucasus are the Pontic mountains in Türkiye and the Hyrcanian forest in Iran.

At the northern edge of the specie's range, the development of *C. sativa* is limited by low temperatures, which cause frost damage and reduced seed production, while at the southern edge, its survival is limited by drought (Freitas et al., 2021). Our study shows that sweet chestnut has a variable preference in terms of climatic requirements, either in Europe or in the Caucasus range (Fig. 2). A marked divergence in the climatic niche between the European and Caucasian populations of the species may be a determinant of the success or failure of AGF (Fig. 2, Table 3). Moreover, the three European distribution areas, which include the Iberian, Apennine, and Balkan peninsulas, represent very different climatic niches of sweet chestnut in terms of precipitation and temperature, and thus have different potential applicability for the Caucasus region (Table 3). According to our results, the Balkan populations experience the most continental climate, with the hottest and driest summer months, while the mesic habitats of the species are in the northern Iberian Peninsula, under the influence of the Atlantic climate (Fig. 2). In addition, the Iberian populations grow within fairly narrow annual temperature ranges, as indicated by the lowest values of the temperature seasonality (bio4) and the highest average isothermality (bio3) compared to the other European populations (Table 3). Spare and isolated populations located in the southern part of the Iberian Peninsula grow under more arid conditions. Conversely, both temperature-related bioclimatic variables (bio3 and bio4) have very different means in the Caucasus compared to the European populations. Moreover, bio4 is practically insignificant for the probability of species occurrence in the Caucasus, whereas it is the key factor for the Iberian populations (contribution >40%). Sweet chestnut also grows at lower annual temperatures in the Caucasus (8.9 °C) compared to the Iberian populations (12.5 °C). Studies show the importance of temperature for the growth and reproduction of the species, making it highly vulnerable to climate change (Freitas et al., 2021; Pérez-Girón et al., 2020). The differences in temperature-related factors probably explain the overall low compatibility between the Iberian and Caucasian populations of sweet chestnut in terms of potential AGF assessed on the basis of climatic factors. A recent study investigating the feasibility of AGF in European beech with Oriental beech also highlighted that the latter experiences much greater annual variation in precipitation and temperature compared to the European species (Kurz et al., 2023).

In the Caucasus and Iberian Peninsula the species occurs in very different habitats in terms of precipitation, which may indicate a higher adaptability of the species to this particular climatic factor. Míguez-Soto

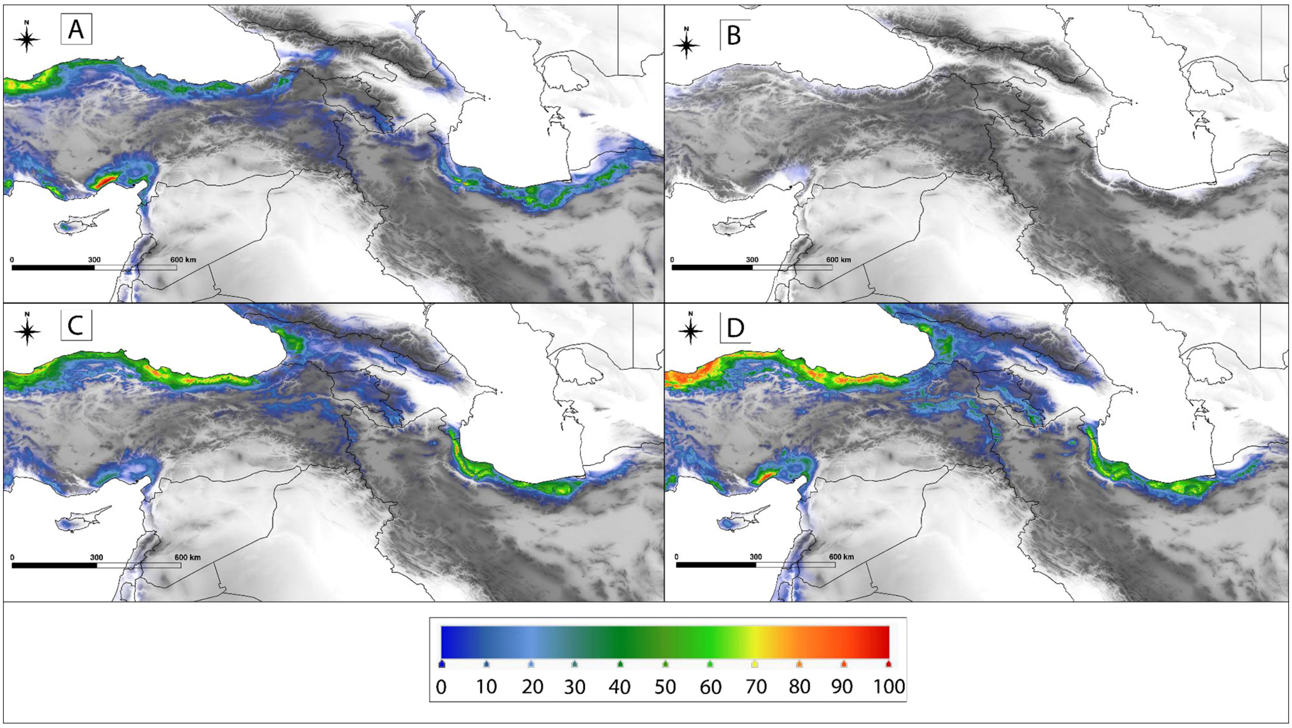

Fig. 4. Maps of theoretical suitable areas for the European populations of *Castanea sativa* in the Caucasus in SSP1-2.6 climate change scenario in period 2071–2100. A) Balkan populations, B) Iberian populations, C) Alpine-Apennine populations, and D) all European; habitat suitability chart in percentages

et al. (2019) demonstrated adaptive variation in the Iberian populations of sweet chestnut, representing xeric and mesophytic ecotypes. Also, within the Caucasus, sweet chestnut grows in a rainfall gradient, with western populations (Colchic) receiving much more rainfall than eastern populations. The average rainfall of the driest month (bio14) in the Colchic area is 116.4 mm, while in the eastern part, it is 40.1 mm and in the Iranian part of the distribution area it is 45.9 mm. Further investigation of the extent of *C. sativa* plasticity and adaptability to annual temperature dynamics in the European-Caucasian range would be important to inform future management, including AGF.

The most appropriate source of AGF in the Caucasus would be populations from the Alpine-Apennine region, and subsequently from the Balkans. The populations from the Alpine-Apennine region shares similar requirements for precipitation (bio14) with the Caucasian area, which makes it more compatible compared to the Balkan populations (Table 3). However, the highest similarity of these two tested gene pools is predicted for the Pontic area, not for the core range in the South Caucasus. In addition, each of the regional gene pools is predicted to be compatible with other parts of the Pontic region. While the Alpine-Apennine populations could be used for the eastern Pontic areas, the Balkan populations could be used in the western Pontic areas. The western Pontic mountains are characterised by a Mediterranean (dry) climate, and the eastern Pontic mountains by a Euro-Siberian (wetter) climate. The physiological, morphological, and genetic studies carried out on the Turkish populations of *C. sativa* revealed a west-east cline following this climatic gradient (Villani et al., 1992). The main differences detected in our work for the Alpine-Apennine and Balkan gene pools relate to the mean temperature of the driest month (bio9), which is much higher in the Balkans than in the Alpine-Apennine range, precipitation of the wettest month (bio13), which is an important predictor of species occurrence in the Alpine-Apennine range but not in the Balkans, and precipitation of the coldest quarter (bio19), which reflects the divergent pattern of annual rainfall in the regions. While in the Balkans rainfall is abundant in late autumn-winter, sweet chestnut in the Alpine-Apennine range experiences less precipitation during the coldest months. However, the use of both regional gene pools would only be effective in the optimistic climate scenario. As climate projections worsen, the suitability of both regional gene pools for the Caucasus region decreases (Figs 4–6).

It appears that, at least based on climate modelling, the eastern part of the sweet chestnut distribution in the South Caucasus, which is most vulnerable to climate change (Beridze et al., 2023a), is not predicted to be suitable for any of the European regional gene pools tested. This is the driest part of the South Caucasus, giving way to the Hyrcanian forests further

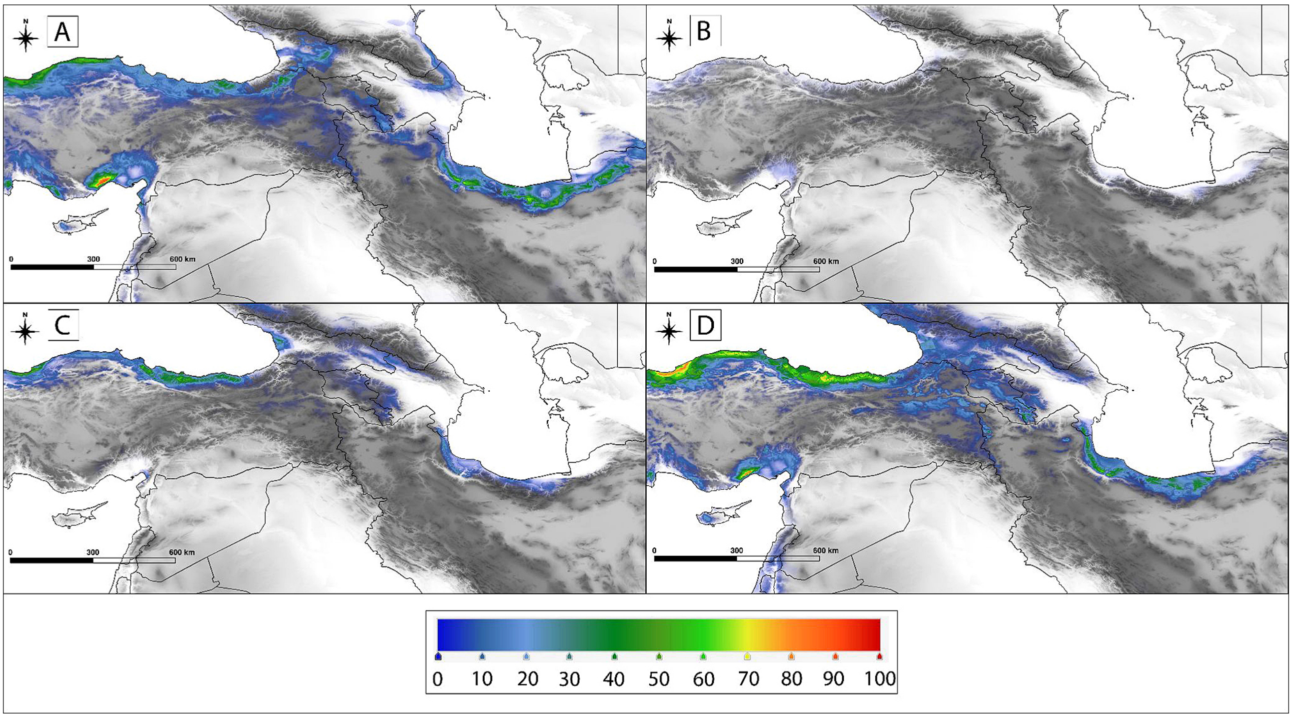

Fig. 5. Maps of theoretical suitable areas for the European gene pools of *Castanea sativa* in the Caucasus in SSP3-7.0 climate change scenario in period 2071–2100. A) Balkan gene pool, B) Iberian gene pool, C) Alpine-Apennine gene pool, and D) all European; habitat suitability chart in percentages

east. The Hyrcanian region could be particularly suitable for the Alpine-Apennine gene pool in the optimistic climate change scenario SSP1-2.6, while Balkan populations would be more suitable in SSP3-7.0. Currently, there are only four relict populations of *C. sativa* in the western Hyrcanian forests (Janfaza et al., 2017). Reconstructions of the possible distribution of the species in the past suggest its presence in the region at least since the last interglacial (120 ka BP) and throughout the Holocene (Beridze et al., 2023b). This is corroborated by a fossil pollen record of *C. sativa* dated to around 3,800 ka BP found in the core of Lake Neor in the Talysh mountains of northwestern Iran (Alinezhad et al., 2021).

In contrast to assisted gene flow, assisted migration - the movement of plants across the landscape into new and climatically suitable areas where they are currently absent - is more controversial because it conflicts with conservation models that favour maintaining current species ranges and *in situ* management. There is also a risk that an introduced species will become either incompatible with the receiving ecosystem or invasive (Twardek et al., 2023). Our models showed that the projected climatic conditions in the coastal part of the Taurus mountains in southern Türkiye would support the growth of sweet chestnut from the Balkan Peninsula, even under the most damaging climate change scenario. Currently, there are no natural or managed stands of sweet chestnut in this region. Fossil pollen records (Roces-Díaz et al., 2018) indicate the presence of the species in the East Mediterranean, but in area covering today's territory of Syria and Lebanon. However, it is possible that these areas could be used in the future for the commercial cultivation of elite genotypes for nut production.

Study limitations

Species distribution modelling are relatively easy to use tools for predicting possible scenarios of species range change, and are therefore widely applied to assist conservationists and forest managers (Mellert & Šeho 2022; Sękiewicz et al., 2020; Freitas et al., 2022; Alipour & Walas 2023). SDMs inherently have some level of uncertainty and limitations that researchers must consider, especially when planning such advanced management strategies as AGF in long-lived tree species. A major appeal of SDMs is that they work by integrating the observational data and bioclimatic predictors to create the statistical models (Zurell et al., 2009). Thus, the quality of the observational data representing the species occurrence in the field affects the prediction of the climatic conditions underlying the species occurrence and thus the modelling of the species niche (Lee-Yaw et al., 2022). Data collection can be biased in several ways affecting the final model (Bryn et al., 2021). In our study, we carefully selected occurrence data from the Caucasus range of the species, and checked

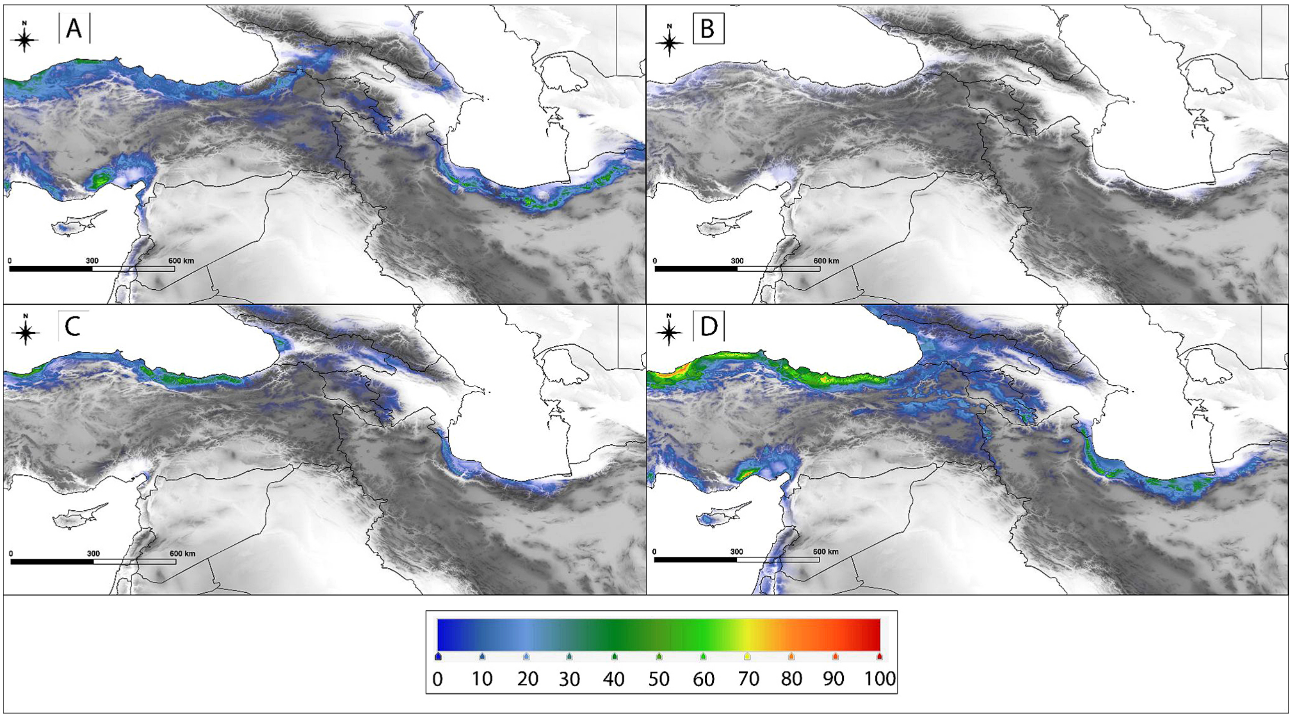

Fig. 6. Maps of the theoretical suitable areas for the European gene pools of *Castanea sativa* in the Caucasus in SSP5-8.5 climate change scenario in period 2071–2100. A) Balkan gene pool, B) Iberian gene pool, C) Alpine-Apennine gene pool, and D) all European; habitat suitability chart in percentages

them manually knowing that the errors and spatial bias (e.g., uneven coverage of the region) may affect the accuracy of results (Bryn et al., 2021). However, the presence/absence of species at a particular site depends on many other non-climatic factors that we could not control for in this study such as demography, competition, local extinction (due to parasites or overexploitation), dispersal ability, human translocation, or feedback mechanisms with the abiotic environment. These factors are crucial to the successful survival and reproduction of a species, but are neglected in climate-based models, such as SDMs. Due to the apparent difference between the realised and the potential niche of the species (Soberón & Arroyo-Peña, 2017), the results of SDMs should always be considered as a first indication of possible risks of species maladaptation to future climates or range reorganisation. Additional important source of uncertainty in SDMs is the climate models used. Discrepancies between different simulations with respect to observations and their predictions of climate change remain significant due to differences in the underlying representation of Earth system processes. Hence, a good practice is to use a range of the projections (Bryn et al., 2021). To account for this uncertainty, we have averaged the results of three of the most recommended climate models for use with the CHELSA (Karger et al., 2021). Furthermore, by choosing CHELSA's climatologies we also intended to address the uncertainty in climatic predictors (explanatory variables) used for distributional modelling. They are also subject to many sources of inaccuracy and error (Lee-Yaw et al., 2022). CHELSA has been shown to perform better in complex landscapes due to a more effective algorithm for downscaling precipitation estimates, which is a critical parameter in determining the distribution of plants (Bobrowki et al., 2021). Finally, SDMs ignore the complexity of the evolutionary responses of populations to environmental change, including the interaction between selection, effective population size, and microevolutionary processes (gene flow, genetic drift, or mutation) that shape adaptive variation.

Final remarks and recommendations for AGF in *Castanea sativa*

The development of management decisions is a complex process and is often case-specific. Certainly, given the risks associated with AGF (outbreeding depression, disruption of non-climatic adaptation, loss of local diversity), genomic assessment of climate-habitat adaptation should be considered to increase the effectiveness of this mitigation measure and avoid failures (Wadgymar et al., 2015; Flanagan et al., 2018; Borrel et al., 2019). As the genomic basis of local adaptation is not yet available for *C. sativa*, other criteria besides the climatic compatibility should be considered when selecting source populations for AGF. Importantly, these should include stands with the highest genetic diversity, reflecting standing genetic diversity as the main sources of evolutionary potential in trees (Barret & Schluter, 2008). Due to its high economic relevance, many genetic studies on *C. sativa* have been carried out on a pan-European or regional scale, providing detailed information on the level of genetic variability useful for future AGF (e.g., Lusini et al., 2014; Cuestas et al., 2017; Mattioni et al., 2017; Chiocchini et al., 2018; Beridze et al., 2023b). It would also be crucial to select populations with no evidence of inbreeding and a large effective population size (Ne), the letter reflecting the rate of genetic erosion and adaptive potential. While direct estimation of these two parameters requires genetic testing, they can also be assessed indirectly. Firstly, studies show that Ne is typically 10% of the census population size, and as such this rule has been proposed to be available to practitioners (Hoban et al., 2020). In addition, historical data on the long-term persistence of populations in the area, a large census population size, stable demographic trends (e.g., vital regeneration and reproduction) and health parameters are good proxies for a large effective population size and thus high genetic diversity. A very useful indication of the genetic composition of populations and their health and demographic status could be the resources of EUFORGEN, in particular the genetic conservation units, which are currently 34 for *C. sativa* in Europe (euforgen.org). AGF should only be considered if there are strong assumptions about local adaptation to climatic conditions (Aitken & Witlock, 2013). The results of provenance trails or common garden experiments, which assess the fitness of populations/genotypes under local and distinct climatic conditions can initially guide AGF planning.

Studies report that ongoing climate change is already disrupting tree reproduction and fruiting patterns, which may affect both seed quantity and quality (Bogdziewicz et al., 2020), potentially making natural tree migration even less effective. On the other hand, local adaptation is ubiquitous among trees, as most of them occupy very large and heterogeneous habitats and are exposed to different selection regimes (Milesi et al., 2019). Thus, to enhance the adaptation process, AGF between populations already adapted to the projected new climatic conditions (e.g., hotter and/or drier habitats) and those lacking beneficial alleles to cope with the expected changes emerges as an attractive strategy to reduce the vulnerability of trees and forests to climate change (Borrell et al., 2020). In the absence of a definitive assessment of the full range of positive and negative outcomes of this management and conservation tool, more knowledge and research are needed before its widespread use in nature.

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