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Exploring the connection between climatic conditions and genetic properties of *Abies alba* Mill., including warm and summer-dry Mediterranean environments

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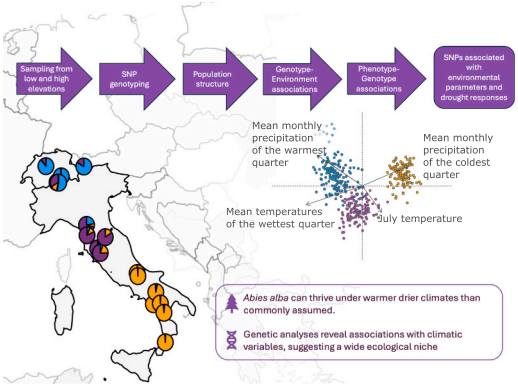
HIGHLIGHTS

- Genotyping reveals genetic alignment of populations from diverse climates.
- Genotype–environment associations indicate drivers of genetic variation in *Abies alba*.
- The climatic niche of *A. alba* reaches warmer temperatures (up to ~25°C July mean temperature) than generally assumed (14-19°C July means).
- Key adaptive genes linked to temperature seasonality and drought are identified.

GRAPHICAL ABSTRACT



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ABSTRACT

Abies alba Mill. is a prominent European tree species predominantly inhabiting cool and humid montane environments. However, paleoecological evidence reveals that during the Eemian and mid-Holocene, *A. alba* thrived in much warmer and drier climates. This capacity is nowadays reflected in cryptic meso- and sub-Mediterranean lowland populations. To link *A. alba* populations across diverse climates spanning from the Mediterranean lowlands to the Alpine timberline, we genotyped 421 specimens from Italy and Switzerland at 190 single-nucleotide polymorphisms (SNPs). Population genetic structure analyses indicate that isolated meso- and sub-Mediterranean lowland populations in Tuscany and Ticino align genetically with higher elevation populations in each region, suggesting that their capacity to thrive in warmer, drier conditions cannot be attributed to plantations with planting stock originating from different climates or to the occurrence of a single warm-adapted lineage showing a disjunct distribution, unless migration between Tuscany and Ticino stands occurred. Genotype–environment associations reveal that temperature seasonality, precipitation during critical seasons, and relative humidity are important for explaining the species' genetic variation. With genotype–environment and genotype–phenotype associations, we identified candidate adaptive genes potentially linked to climatic conditions and drought response. While certain adaptive alleles may have spread from Tuscany and Southern Italy or could be explained by a shared ancestry of Ticino and Tuscan populations, local adaptation may have occurred at specific loci. These findings underscore the importance of considering the hitherto overlooked lowland Mediterranean populations of *A. alba* to better understand the species' climatic niche and its potential for forest conservation and management under global warming.

1. Introduction

Climate change stands as a global challenge, casting detrimental effects on societies and ecosystems (IPCC, 2023; Vacek et al., 2023). Global warming has resulted in increased frequency and severity of heat waves and drought events in most Mediterranean and temperate zones (Venegas-González et al., 2022), threatening forests and other vegetation types by altering their environmental conditions, such as soil and air moisture and temperature conditions, and affecting the timing of the growing seasons (Vacek et al., 2023). Due to their long regeneration time, forest trees face difficulties in adapting to rapid environmental changes (Dauphin et al., 2021; Depardieu et al., 2021). For instance, drought-induced forest deterioration associated with global warming has already emerged (Camarero et al., 2011; Cherubini et al., 2021), affecting even drought-adapted Mediterranean trees such as *Quercus ilex* L. (Alderotti et al., 2023). In this context, global warming has the potential to cause substantial shifts in the European vegetation (Rey et al., 2020).

Adaptive variation plays a crucial role in the spatial distribution of species and their potential to cope with future climates (Salloum et al., 2022). Genotype–environment association (GEA) research is providing an important basis for advancing forest management and conservation in the face of accelerating global warming (Fady et al., 2016). As a result, an increasing number of studies are being conducted to identify adaptive genes and the underlying environmental drivers, seeking evidence of local adaptation in forest ecosystems (Feng et al., 2024). An expanding body of research has also explored the genetic associations with drought and heat stress resistance in forest trees (Csilléry et al., 2020; Leites and Benito Garzón, 2023).

Silver fir (*Abies alba* Mill.) is considered a keystone species to maintain biodiversity and ecosystem services in temperate European forests (de Rigo et al., 2017). It is a functional balancer that stabilizes soils and is relatively resistant to windthrow and snow and ice breakage (Dobrowolska et al., 2017). Furthermore, it produces timber with a high economical value and forms protection forests for settlements, roads, and railways in mountainous areas (Tinner et al., 2013). *Abies alba* has received considerable attention in climate change research and for its potential use in new areas because it displays a marked difference between current and past realized climatic niches, indicating that the species might have a greater potential to cope with climate change than expected from its currently assumed ecological requirements (Tinner et al., 2013; Vitasse et al., 2019; Zagwijn, 1996).

Today, the main range of *A. alba* spans from 40°N to 52°N latitude and from 5°E to 27°E longitude, with isolated occurrences extending the western limit to 1°W and the southern limit to 38°N (Wolf, 2003), and with a broad altitudinal distribution from around 40 m a.s.l. close to Pisa in Tuscany, Italy (Walder et al., 2021), to about 2900 m a.s.l. in the Pirin Mountains in Bulgaria (Tashev and Tsavkov, 2014; Wolf, 2003). Within this range, occurrences are concentrated at intermediate to high elevations (500–2000 m a.s.l.; Mauri et al., 2016), commonly forming mixed stands with *Fagus sylvatica* L. or *Picea abies* (L.) H. Karst. and occasionally in association with *Pinus sylvestris* L., *Quercus robur* L., *Acer* sp., or *Carpinus betulus* L. (Lang et al., 2023). The species currently thrives in climates with mean annual temperatures ranging from approximately 7 to 13 °C or mean July temperatures from 14 to 19 °C and is predominantly found in regions where annual precipitation exceeds 800–1000 mm (Mayer, 1984; Tinner et al., 2013).

Paleoclimatic and paleoecological evidence suggests a substantially different past climatic niche (Tinner et al., 2013; Vitasse et al., 2019). The species *A. alba* has evolved in Europe during the Miocene (Badenian or Langhian) approximately 16–15 millions years ago, in competition with subtropical evergreen broadleaved trees (e.g., of the genera *Phoebe*, *Laurus*, *Symplocos*, *Toddalia, Mastixia, Ficus*, *Tetrastigma*, *Buxus, Ceratonia, Olea,* evergreen *Quercus* and palms), when temperatures were >5 °C warmer than today (Lee et al., 2023; Mai, 1995). The species survived the glacial–interglacial cycles of the Quaternary in Europe and was more widespread during the Eemian, 130,000–115,000 years ago, with temperatures at least 1–2 °C higher than today (Beaudouin et al., 2005; Kaspar et al., 2005; Zagwijn, 1996). Furthermore, fossil evidence reveals that during the Holocene Thermal Maximum (HTM), approximately 10,000–5000 years ago, *A. alba* coexisted with *Quercus pubescens* Willd., *Q. petraea* (Matt.) Liebl., *Q. cerris* L., *Ulmus* sp., and *Tilia* sp. in the sub-Mediterranean forelands of the Southern Alps and the Northern Apennines (Gobet et al., 2000; Tinner et al., 2013; Vescovi et al., 2010), and with *Quercus ilex* and other Mediterranean species in meso-Mediterranean forests close to the shore of the Mediterranean Sea in Tuscany (Colombaroli et al., 2007; Henne et al., 2013; Tinner et al., 2013; Vitasse et al., 2019), under significantly warmer climates than in its current range (e.g., mean July temperatures 24–26 °C; Tinner et al., 2013; Vitasse et al., 2019).

The presence of *A. alba* in Mediterranean lowlands in Central Italy has been reported, even at sea level in Tuscany (Giacobbe, 1949, 1950). Such observations and peculiar phenotypic traits led ecologists to hypothesize the existence of a drought-adapted, warm-loving Mediterranean subspecies, *A. alba* subsp. *apennina* Brullo, Scelsi & Spamp (Brullo et al., 2001; Giacobbe, 1949, 1950). The presence of meso-Mediterranean *A. alba* populations, such as those at Varramista in Tuscany near to the Mediterranean Sea, is in agreement with the HTM and

Eemian occurrence of the species. Although these stands were planted at the beginning of the 19th century (Cortini Pedrotti, 1967), population genetic analyses revealed that they share the same lineage as nearby Tuscan stands that show Central Apennine origins, with an admixture from Northern and Southern Italy (Coşgun et al., 2025). These ecologically enigmatic Mediterranean stands of Varramista can thrive in competition with evergreen *Q. ilex* at a mean July temperature of 24.5 °C, which surpasses the upper temperature limit of its current known range by approximately 5–6 °C, under dry summer conditions (97.4 mm sum of June, July, August; Walder et al., 2021).

New field surveys have led to the discovery of two additional cryptic meso-Mediterranean stands at Poggio Antico (~540 m a.s.l.) and Tavernelle (~380 m a.s.l.) in Tuscany, Italy, and two cryptic sub-Mediterranean stands at Corcapolo (~340 m a.s.l.) and Arcegno (~430 m a.s.l.) in Ticino, Switzerland (Coşgun et al., 2025), so that the formerly unique stands of Varramista can be compared with other warm-loving populations. By cryptic, we refer to populations that exist in small, isolated stands under untypically warm and dry climatic conditions and that are unknown or neglected in the modern ecological literature. However, despite the existence of such cryptic sub-Mediterranean and meso-Mediterranean stands, there is no current knowledge of whether this warm-adapted ecological behavior is associated with a specific genetic signature.

Here, we focus on the climate-associated genetic variation in cryptic meso-Mediterranean and sub-Mediterranean *A. alba* populations. Our goal is to deepen the understanding of the climatic niche of *A. alba* ecotypes in such particularly warm and dry environments. Through genotype–environment and genotype–phenotype association analyses, involving the genotyping of single-nucleotide polymorphisms (SNPs) of specimens across a wide latitudinal and altitudinal gradient, from Southern Switzerland to Southern Italy and from the Alpine timberline to the Mediterranean lowlands, we aim to identify the drivers of genetic variation across diverse climates. Genotype–environment association analyses mainly rely on the comparison with publicly available climatic data (Brun et al., 2022; Karger et al., 2017, 2018) as well as own microclimatic measurements, while genotype-phenotype associations mainly rely on tree-ring data from an own parallel study (Mazza et al., under review). Additionally, we seek to discover candidate adaptive genes that might enable genetic lineages of *A. alba* to thrive in atypically warm and dry conditions.

2. Methods

2.1. Study design and sampling

The lowland cryptic *A. alba* stands in Tavernelle and Poggio Antico (Tuscany, Italy) were detected by local owners and residents and subsequently explored through field surveys accompanied by the regional forestry agency as part of the present and a previous study (Coşgun et al., 2025). These lowland stands have a plantation history dating back to the early 20th century. Because the origin of the planted individuals is unknown and as there is no active silvicultural intervention today, the current stands reflect the natural regeneration of trees of unknown geographical provenance. Surveys in Ticino (Switzerland) led to the discovery of hitherto unknown lowland sub-Mediterranean stands. Unfortunately, only the stand in Corcapolo presented a sufficient population size to be considered in the study (for further details; Coşgun et al., 2025).

Field campaigns were carried out in the summers of 2021 and 2022 to collect genetic material (needles), information on soil structure, and to place temperature data loggers. Genetic materials of *A. alba* were collected through random sampling within individual stands, while the selection of stands was based on predetermined strata (latitudinal, altitudinal, and environmental gradients). Samples were collected from *A. alba* individuals in 22 stands originating from natural regeneration or plantation across a wide latitudinal range spanning from Serra San Bruno in Southern Italy (38.55°N) to Anzonico in Southern Switzerland (46.43°N) and spanning over altitudinal gradients from Varramista (around 45 m a.s.l.) to Abetone (around 1448 m a.s.l.) in Tuscany and from Corcapolo (around 340 m a.s.l.) to Pizzo Ruscada (around 1859 m a.s.l.) in Ticino (Fig. 1, Tables 1 & S1). In addition, we sampled Grisons and Bern stands representing south-eastern and western Swiss populations, respectively. Within each stand, needles were collected from ca. 20 adult and young trees per stand randomly selected after forcing a distance of at least 20 m from the previously sampled specimen to avoid sampling closely related trees. For small *A. alba* stands, the number of specimens was reduced (Table 1). *Abies alba* specimens collected by Walder et al. (2021) were also included to represent Varramista stands.

2.2. DNA extraction and SNP genotyping

The *A. alba* DNA samples used in this study were prepared as part of our previous study (Coşgun et al., 2025). DNA extractions were performed using ~25 mg lyophilized and ground needle tissue per sample using the sbeadex maxi plant kit (LGC Genomics, Berlin, Germany) according to the manufacturer's protocol. DNA quality and quantity were assessed with a NanoDrop spectrometer (Thermo Fisher Scientific, Waltham, Massachusetts, U.S.). A total of 478 *A. alba* DNA extractions were genotyped for our previous study using KASP arrays (LGC Genomics, Berlin, Germany) at 174 putatively neutral single-nucleotide polymorphisms (SNPs) from Roschanski et al. (2016). Moreover, in this study we genotyped 16 SNPs identified within candidate adaptive genes, characterized through the transcriptomes of Behringer et al. (2015), as detailed in Supplementary Materials 1 & 2. After excluding populations without local climate data and redundant populations, 421 genotypes from Coşgun et al. (2025) were used for further biostatistical analyses in this study.

2.3. Environmental analyses

During field campaigns, one or two Onset HOBO Pendant® data loggers were placed per sampling site to record local temperature. Data loggers were installed on the north sides of the trees in shade and ~ 2 m above ground level. Across all populations surveyed, 38 data loggers were placed at different elevations, and local temperatures were recorded for one year at 2-h intervals (Table S3). To test logger accuracy, we placed one additional data logger in the experimental garden of the Swiss Federal Institute for Forest, Snow and Landscape Research (WSL Cadenazzo, Switzerland), and the temperature records were collated

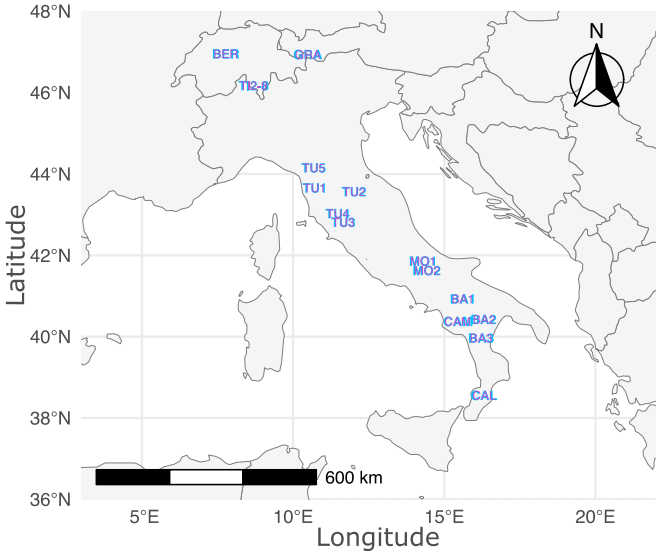

Fig. 1. Localities of the *Abies alba* stands sampled for this study.

Table 1
Coordinates, elevations, July temperatures, and sample sizes for the studied stands of *Abies alba*.

Stand name	Abbreviation	Location	Coordinates (°North-East)	Elevation (m a.s.l.)	July temperature* (°C)	Annual precipitation* (mm)	Sample size
Bern	Ber	Dürsrütiwald, Bern, CH	46.961–7.777	900	18.8	1376	20
Graubünden	Gra	Valsot, Grisons, CH	46.937–10.481	1258	17.1	706	20
Ticino2	Ti2	Corcapolo, Ticino, CH	46.173–8.693	340	23.1	1897	20
Ticino3	Ti3	Intragna, Ticino, CH	46.181–8.677	945	19.4	1757	18
Ticino4	Ti4	Intragna, Ticino, CH	46.181–8.635	1250	16.9	1683	20
Ticino5	Ti5	Corte Nuovo, Ticino, CH	46.179–8.594	1818	13.6	1545	14
Ticino6	Ti6	Pizzo Ruscada, Ticino, CH	46.179–8.592	1859	13.2	1535	11
Ticino7	Ti7	Bosco Negro, Ticino, CH	46.187–8.564	1437	15.8	1637	20
Ticino8	Ti8	Anzonico, Ticino, CH	46.433–8.867	1250	18.7	1283	11
Tuscany1	Tu1	Varramista, Tuscany, IT	43.658–10.715	45	24.6	843	32
Tuscany2	Tu2	Tavernelle, Tuscany, IT	43.546–12.014	383	22.7	816	20
Tuscany3.1	Tu3.1	Pigelleto (Natural), Tuscany, IT	42.811–11.658	768	22.2	731	24
Tuscany3.2	Tu3.2	Pigelleto (Plantation), Tuscany, IT	42.811–11.658	833	22.2	731	22
Tuscany4	Tu4	Poggio Antico, Tuscany, IT	43.027–11.474	537	23.8	757	20
Tuscany5	Tu5	Abetone, Tuscany, IT	44.152–10.679	1448	17.9	1396	20
Molise1	Mo1	Pescopennataro, Molise, IT	41.866–14.294 41.851–14.291	1249–1471	18.4	990	20
Molise2	Mo2	Collemeluccio, Molise, IT	41.709–14.355	885	20.6	952	20
Basilicata1	Ba1	Monticchio, Basilicata, IT	40.930–15.615	677	22.9	918	9
Basilicata2	Ba2	Laurenzana, Basilicata, IT	40.406–15.958	1118	19.5	880	20
Basilicata3	Ba3	Terranova di Pollino, Basilicata, IT	39.966–16.217	1441	20.1	1758	20
Campania	Cam	Monte Motola, Campania, IT	40.374–15.460	1138	20.9	1355	20
Calabria	Cal	Serra San Bruno, Calabria, IT	38.557–16.314 38.547–16.289	823–1071	21.4	1632	20

* July temperatures were obtained through on-site temperature data loggers for the years 2021–2022 and 2022–2023 (for Switzerland and Italy, respectively; Table S4). Annual precipitation was obtained through nearby meteorological stations (Table S5).

with the data from the neighboring MeteoSwiss Magadino/Cadenazzo weather station (Fig. S1).

To specify the bioclimatic differences among lowland sub-Mediterranean and meso-Mediterranean populations and the stands from the commonly assumed ecological range, we employed the bioclimatic variables defined in WorldClim (Hijmans et al., 2005). Bioclimatic variables from downscaled climatic data were obtained from CHELSA BioClim and BioClim+ (Brun et al., 2022; Karger et al., 2017, 2018) to represent macroclimatic conditions for the period 1981–2010. Mean July temperatures were also obtained through CHELSA V2.1 for the period 1981–2010 to represent the same period as the bioclimatic variables (Table S2, Supplementary material 2-CHELSA Bioclim). To check climate results from downscaled modeling and to gain insight into microclimate, data recorded by Onset HOBO Pendant® data loggers were employed for re-calculating temperature-related bioclimatic variables according to WorldClim (Hijmans et al., 2005). Monthly precipitation values were obtained through the MeteoSwiss–Swiss Federal Office of Meteorology and Climatology (https://www.meteoswiss.admin.ch/), SIR–Tuscany Regional Hydrological Service (http://www.sir.toscana.it/) and SCIA–National System for the Processing and Dissemination of Climate Data Italy (https://scia.isprambiente.it/). Bio1-Bio19 (except Bio15) variables and growing season precipitation were re-calculated (Table S5, Supplementary material 2-Logger-Bioclim). These two climate datasets (CHELSA vs. Loggers/Station) will be hereafter referred to as macroclimate and microclimate, respectively.

Soil profiles of the study sites were also investigated during the fieldwork. Soil samples were extracted with a soil corer with a diameter of 10 cm to the greatest possible depth, and the soil texture was determined on-site following Thien (1979), and checked with Hengl et al. (2017). Bettoni et al. (2023) and Walder et al. (2021) were also consulted for calibrating the soil texture of the respective study sites. In addition, the rooting depths were obtained through the "Digital Soil Suitability Map of Switzerland – Root Penetration Depth" of the Swiss Federal Office for Agriculture (FAOG) and the "Soil Rooting Depth Map of Italy" (Rivieccio et al., 2020), compared with the on-site determination. The lower rooting depth was selected to calculate soil available water capacity (AWC; Supplementary material 2-Soil). AWC values for the study sites were obtained through the USDA soil textural triangle and with the corresponding field capacity and permanent wilting point (Rawls et al., 1992), calculating the bucket sizes according to Henne et al. (2011).

2.4. Statistical analyses

2.4.1. Population structure

Genetic structure was assessed using the Bayesian clustering algorithm implemented in the software STRUCTURE v.2.3.4 (Falush et al., 2003, 2007; Hubisz et al., 2009; Pritchard et al., 2000) with 100,000 burn-in and 1,000,000 Markov Chain Monte Carlo iterations, by choosing the LOCPRIOR model together with the admixture and correlated allele frequencies options based on 174 putatively neutral SNPs. For each K in the range of 1–10, ten iterations were run, and the STRUCTURE output was subjected to the greedy and large greedy algorithms in CLUMPP (Jakobsson and Rosenberg, 2007), as implemented in CLUMPAK (Kopelman et al., 2015) via Structure selector (Li and Liu, 2018). Further details are described in Coşgun et al. (2025).

2.4.2. Genetic associations to climate as inferred from CHELSA and logger data

The association between environmental variables and genetic variation was investigated with both CHELSA and logger-station bioclimatic variables, considering neutral population structure. Firstly, distance-based redundancy analysis (dbRDA) was implemented following Benestan et al. (2021). Principal Coordinates Analysis (PCoA) was performed on the genetic matrix of the putatively neutral SNPs from Roschanski et al. (2016), and PCoA components were employed as the response variables in dbRDA. We then computed Moran's Eigenvector Maps (MEMs) to represent spatial variables in the explanatory variables together with the environmental variables. Variables with high correlations (Bio1, Bio2, Bio5, Bio6, Bio10, Bio11, Bio12, Bio16, Bio17, Maximum monthly Near-Surface Relative Humidity (HURS max), HURS mean, Growing Season Length (GSL), Monthly Climate Moisture Index (CMI)) were removed for dbRDA to avoid multicollinearity. Secondly, Gradient Forest (Ellis et al., 2012), a random forest-based machine learning algorithm, was implemented with allelic frequencies as response variables and all bioclimatic variables, including correlated ones, as predictors. We followed Pitcher et al. (2011) to run five replicates with 5000 trees and a correlation threshold of 0.7. Two random variables were also added to environmental variables for dbRDA and Gradient Forest to test the accuracy of the analyses. In addition, to investigate more specifically the Tuscany populations that represent the warmest and driest Mediterranean sampled area, a separate dbRDA was performed for these samples, with ecological indicator values for light, moisture, temperature, reaction, nutrient, and slope (Table S6) derived from vegetation surveys, in addition to the bioclimatic variables (CHELSA and local loggers/station data).

Using the entire set of 190 SNP markers, we employed several methods to identify the loci associated with environmental variables. Firstly, we identified outlier loci based on population genetic inference using BayeScan v.2.1 (20 pilot runs of 5000 iterations each and a burn-in of 50,000 cycles, 10 prior odds for the neutral model) and applying a threshold on q-values lower than 0.05 (Foll and Gaggiotti, 2008). In addition, the analytical pipeline "Detect loci under selection from F-statistics" in Arlequin v.3.5 (Excoffier et al., 2009; Excoffier and Lischer, 2010) was run using default parameters (20,000 simulations with 100 demes per group), and loci with F_{ST} –heterozygosity values that fall outside of the 99 % confidence interval and have a p-value lower than 0.05 were identified as outliers. In the second step, BayeScEnv (de Villemereuil and Gaggiotti, 2015) and RDA were implemented to identify the loci associated with climatic conditions by employing environmental variables as explanatory factors. Genotyping results were converted using PGDSpider (Lischer and Excoffier, 2011), and BayeScEnv was run on each bioclimatic variable with default parameters (burn-in of 50,000 cycles, 20 pilot runs with a length of 2000, upper bound for g: 10, mean prior for alpha: −1, prior probability for non-neutral models: 0.10, prior preference for the locus-specific model: 0.5) to identify the loci with a F_{ST}-value significantly associated with the environmental variables. SNPs with a q-value lower than 0.05 for tests of local adaptation (g parameter) were considered as candidate adaptive loci. For the RDA, the R code of Benestan et al. (2016) was run with the following modifications; employing Mahalanobis distance for outlier detection and also looking for moderate correlation (< -0.40 and > 0.40). We then kept the candidate adaptive loci that were identified by at least one of two population genetic inference methods (BayeScan and Arlequin) and one of two environmental association methods (BayeScEnv and RDA, Fig. S5). For these SNPs, F_{ST}-values were calculated for young (Diameter at Breast Height (DBH) < 20 cm) and adult (DBH >20 cm) trees based on Wright (1949).

2.4.3. Genetic associations to drought as inferred from tree-rings

The association between genetic variation and drought responses was studied for seventeen specimens from the Varramista stand. For the extreme drought years, the resistance (Rt; the ability to avoid growth reduction during drought), the recovery (Rc; the increase in growth relative to the minimum growth during drought), and the resilience (Rs; the capacity to reach the pre-drought growth level) were inferred from available tree-ring data (Mazza et al., under review) according to Fekedulegn et al. (2003) and Martín-Benito et al. (2008), and were used for genotype–phenotype associations. Using genotypes and the individual drought response indices, we applied "all-relevant" and "minimal-optimal" feature selections based on Nilsson et al. (2007), employing the random forest-based R packages VSURF (Genuer et al., 2015) and Boruta (Kursa and Rudnicki, 2010). VSURF was performed using default settings with 2000 trees in each forest, and the associated SNPs were identified in the prediction step based on out-of-bag (OOB) error rates from nested random forests. We also performed Boruta using default parameters, except that the maximum number of iterations was increased to 500 to reduce the number of tentative predictors. In addition, a univariate general linear model was implemented in Tassel V5 (Bradbury et al., 2007) with 10,000 permutations to obtain adjusted p-values independent of the data distribution.

3. Results

3.1. Population genetic structure

STRUCTURE analysis reveals three genetic clusters with a clear geographical distribution, i.e., Northern Italy/Switzerland, Central Italy, and Southern Italy (Fig. S2 & Fig. S3). With two genetic clusters ($K = 2$), STRUCTURE analysis splits the studied populations into Southern Italy and the rest (i.e., Central Italy, Northern Italy/Switzerland; Fig. S3), while Tuscan populations represent an admixture of Northern Italian/Swiss and Southern Italian populations. The model fit for three clusters (K) was higher than for $K = 2$, with the apparent separation of Tuscan populations, still with some admixture from Northern Italian/Swiss and Southern Italian populations. The only Tuscan stand with no sign of admixture is Poggio Antico (Tu4). For $K = 4$, identified as the most likely number of clusters (for further details; Coşgun et al., 2025), Poggio Antico (Tu4) represents a separated genetic cluster. Besides this, the meso-Mediterranean populations in Tuscany reflect the regional genetic structure and do not show any genetic specificities in comparison with their neighboring stands at higher elevations. Similarly, the warmest sub-Mediterranean site of Ticino Corcapolo (Ti2) is assigned to the same genetic cluster as the Alpine *A. alba* in the region and with other Swiss populations (Bern and Grisons) but shows substantial admixture with Tuscan and Southern Italian populations (Fig. S3).

3.2. Environmental variables driving genetic variation

To identify the climatic variables associated with genetic variation among sampled *A. alba* populations, two different methods of genotype–environment associations were implemented. dbRDA with bioclimatic variables from CHELSA to represent macroclimate explains 17.6 % of the genetic variation ($p = 0.001$). Specifically, 14.4 % of the genetic variation is explained by population structure (ancestral coefficients at $K = 3$) and geographic distances (Fig. 2, Table S7). Macroclimatic variables that explain the remaining 3.2 % of the genetic variance are Bio8 (mean daily mean air temperatures of the wettest quarter), SWB (soil water balance), GSP (accumulated precipitation amount on growing season days), GST (mean temperature of the growing season), Bio4 (temperature seasonality), HURS range (annual range of monthly near-surface relative humidity), Bio7 (annual range of air temperature), Bio18 (mean monthly precipitation amount of the warmest quarter), July temperature, Bio15 (precipitation seasonality), and Bio3 (isothermality). To analyze the driving effects of microclimate, the second dbRDA used bioclimatic variables re-calculated with data recorded by temperature data loggers and obtained through meteorological stations. With this analysis, we obtained similar explanatory variables as with macroclimate, such as Bio18, Bio14, AWC (available water capacity),

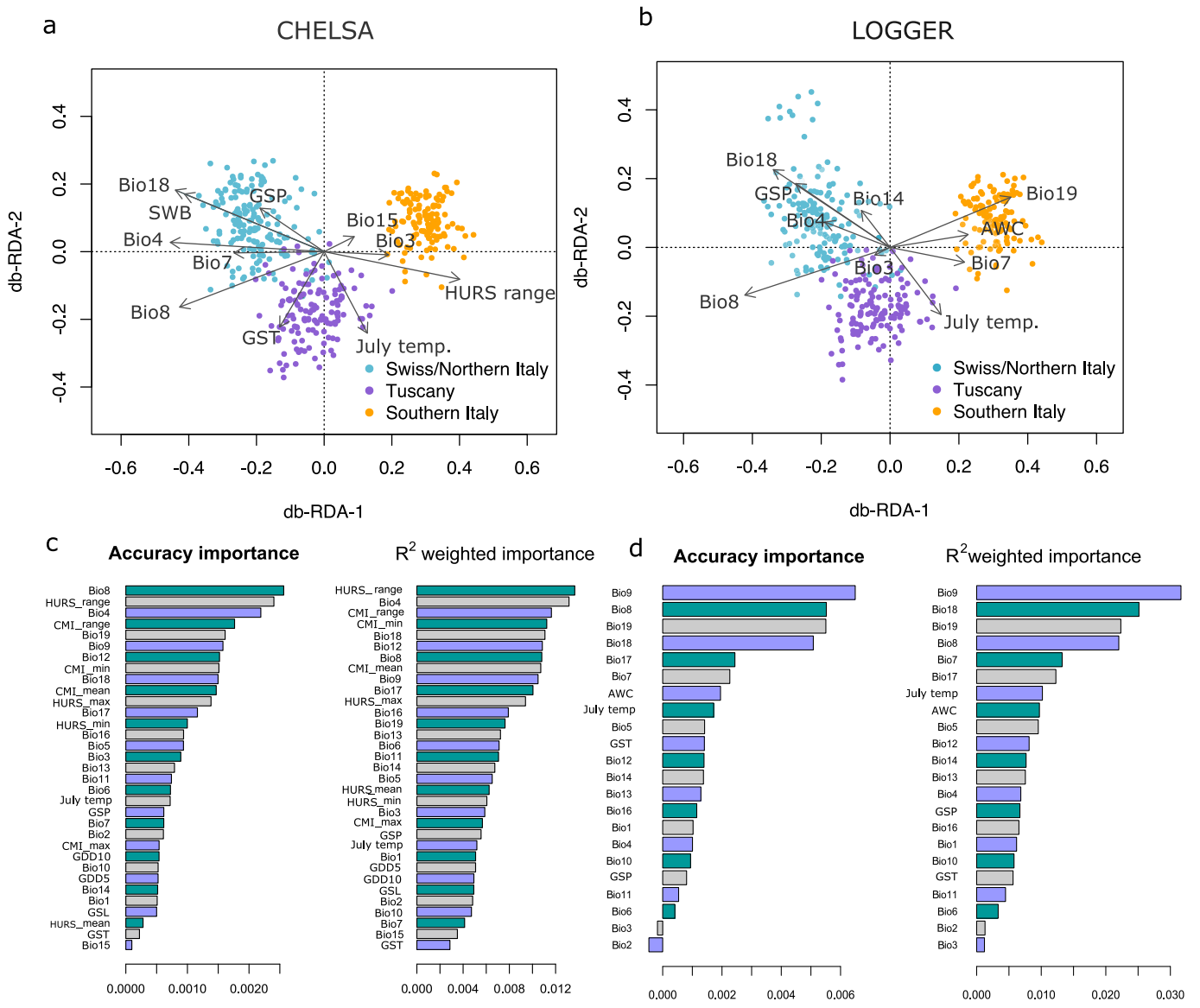

Fig. 2. Biplots of genetic variation in *Abies alba* on dbRDA axes 1 and 2. Arrows represent significant bioclimatic variables based on CHELSA (a) and on-site temperature measurements or interpolation from nearby weather stations (b); accuracy and R^2 weighted importance of bioclimatic variables based on CHELSA (c) and on-site temperature measurements or interpolation from nearby weather stations (d) (Bio3: isothermality, Bio4: temperature seasonality, Bio7: annual range of air temperature, Bio8: mean daily mean air temperatures of the wettest quarter, Bio9: mean daily mean air temperatures of the driest quarter, Bio15: precipitation seasonality, Bio18: mean monthly precipitation amount of the warmest quarter, Bio19: mean monthly precipitation amount of the coldest quarter, HURS range: annual range of monthly near-surface relative humidity, July temp: July temperature, SWB: soil water balance, GST: mean temperature of the growing season, GSP: accumulated precipitation amount on growing season days, CMI: the climate moisture index, AWC: available water capacity).

Bio7, Bio8, July temperature, GSP, and Bio19 (mean monthly precipitation amount of the coldest quarter) with similar explanatory power (3.6 % of the genetic variation).

In the first analysis with bioclimatic variables directly obtained from CHELSA to represent macroclimate, Gradient Forest identifies HURS range, Bio4, CMI range (annual range of monthly climate moisture index), CMI min (minimum monthly climate moisture index), and Bio18 as relevant variables based on their ranked importance. When we perform the second Gradient Forest analysis with bioclimatic variables derived from temperature data loggers to represent microclimate, Gradient Forest selected Bio9 (mean daily mean air temperatures of the driest quarter), Bio18, Bio19, Bio8, and Bio7 (Fig. 2, Table S8).

dbRDA for Tuscany identifies additional environmental driving factors (Fig. 3). While reaction (soil pH), SWB, Bio19 (mean monthly precipitation amount of the coldest quarter), HURS range, nutrient, and Bio15 explain 7.8 % of the genetic variation of *A. alba* in Tuscany, AWC, Bio4, reaction, nutrient, and Bio3 account for 7.6 % in the microclimatic dataset.

3.3. SNPs associated with environmental variables

BayeScan identifies 30 SNPs as outliers with a q-value <0.05, including three candidate adaptive genes we had selected for this study based on transcriptomes published in Behringer et al. (2015). Using F-statistics in Arlequin, we identify 54 SNPs with a p-value <0.05, with nine of them, including one within our newly identified candidate adaptive genes, placed outside the 99 % confidence interval in the F_{ST}–heterozygosity curve (Supplementary Material 2-Outliers). The four SNPs contig14580_627, contig00716_144, newcontig07067_53, and aalba5_s00278571_11484 are determined as outliers by both BayeScan and Arlequin.

Nine candidate loci are identified by BayeScEnv and/or RDA, in

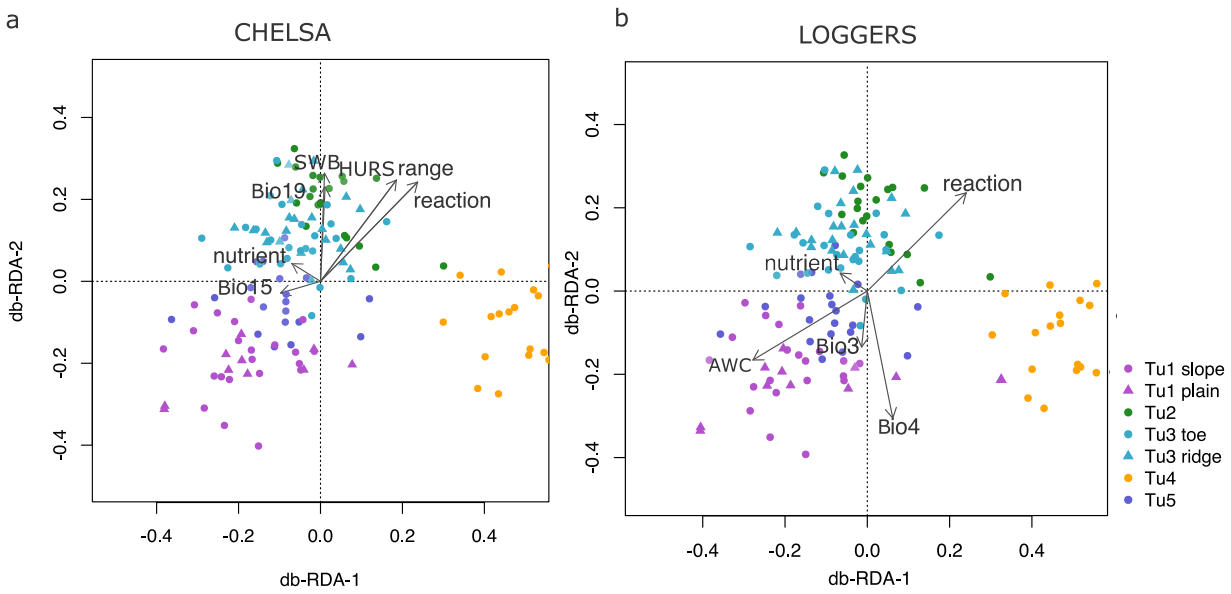

Fig. 3. Biplots of genetic variation in *Abies alba* from Tuscany. Arrows represent significant bioclimatic variables based on CHELSA (a) and on-site temperature measurements or interpolation from nearby weather stations (b) (bio3: isothermality, bio15: precipitation seasonality, bio19: mean monthly precipitation amount of the coldest quarter, HURS range: annual range of monthly near-surface relative humidity, SWB: soil water balance, AWC: available water capacity, Tu1: Varramista, Tu2: Tavernelle, Tu3: Pigelleto, Tu4: Poggio Antico, Tu5: Abetone).

Table 2
Outlier SNPs associated with climatic variables in *Abies alba*. (Bio3: isothermality, Bio4: temperature seasonality, Bio8: mean daily mean air temperatures of the wettest quarter, Bio10: mean daily mean air temperatures of the warmest quarter, Bio15: precipitation seasonality, Bio18: mean monthly precipitation amount of the warmest quarter, Bio19: mean monthly precipitation amount of the coldest quarter, HURS range: annual range of monthly near-surface relative humidity, SWB: soil water balance, GSP: accumulated precipitation amount on growing season days).

SNP ID	Associated environmental parameter	Protein	SNP source reference	Function
contig00716_144 [a,b,bv,r]	GSP, Bio4, Bio8, Bio18, Bio19, HURS range, SWB	Stromal 70 kda heat shock-related chloroplastic-like	Roschanski et al. (2016)	stomatal closure and seed germination (Chun et al., 2021), protein transport and regulation, denatured protein refolding (Ding et al., 2022; Lee and Schöffl, 1996)
contig14580_627[a,b,r]	HURS range, Bio4, Bio18	ATP-dependent Clp protease proteolytic subunit-related protein	Roschanski et al. (2016)	degradation of misfolded or damaged proteins (Ali and Baek, 2020)
aalba5_s00278571_11484 [a, b,bv]	HURS range	Auxin-induced protein	This study	seed dormancy, root patterning, cell differentiation, flower organ development, regulation of root architecture, ABA-responsive gene expression, protein modification, signal transduction, ROS metabolism, metabolic homeostasis (de María et al., 2020; Shi et al., 2014)
contig14580_865[b,r]	HURS range, Bio4, Bio18	ATP-dependent Clp protease proteolytic subunit-related protein	Roschanski et al. (2016)	degradation of misfolded or damaged proteins (Ali and Baek, 2020)
newcontig00575_232[b,bv]	HURS range	Glyceraldehyde-3-phosphate dehydrogenase b subunit	Roschanski et al. (2016)	energy production, DNA repair, transcriptional regulation, sugar and amino acid balance, embryo development, viable pollen development, root growth, and ABA signal transduction as a critical enzyme in the glycolytic pathway (Li et al., 2019)
contig16822_456[b,bv]	HURS range, Bio15, Bio19	Serine/threonine protein phosphatase 2A	Roschanski et al. (2016)	growth and stress signalling, stomatal closure and modulating downstream genes (Cutler et al., 2010)
contig24145_82 [b,bv]	HURS range, Bio3	60S ribosomal protein l7–4-like	Roschanski et al. (2016)	peptide bond formation (Fakih et al., 2023)
aalba5_s00068877_34157[b, bv]	Bio10, Bio3	WRKY 10	This study	regulate stress signalling as well as drought and cold stress response (Fei et al., 2018; He et al., 2016; Zhang et al., 2022)
newcontig08206_228 [b,r]	Bio8	Phospho-2-dehydro-3-deoxyheptonate aldolase	Roschanski et al. (2016)	involved in shikimate/chorismate /amino acid/aromatic amino acid family biosynthetic processes (Pan et al., 2017)
contig08248_183[t]	HURS range, reaction	PIP1 aquaporin	Roschanski et al. (2016)	promoting water transport diffusion across membranes by regulating hydraulic or osmotic permeability (Li et al., 2014)

[a]Arlequin.
[b]BayeScan.
[bv]BayeScEnv.
[r]RDA.
[t]Tuscany RDA.

addition to BayeScan and/or Arlequin. The highest number of associations are found for the HURS range, followed by Bio3, Bio4, and Bio18 (Table 2). BayeScEnv identifies six outlier SNPs with a q-value <0.05, while RDA detects four outlier SNPs with a correlation >0.4 or < −0.4. The three SNPs, contig14580_627, contig14580_865, and newcontig08206_228, are selected by RDA but not BayeScEnv. The SNP in the gene encoding for the protein stromal 70 kda heat shock-related chloroplastic-like (contig00716_144) is identified by both BayeScEnv and RDA and is associated with several environmental variables such as GSP, Bio8, Bio18, Bio19, HURS range, SWB. RDA for Tuscany also identifies an additional SNP (contig08248_183) correlated with the HURS range and reaction.

3.4. SNPs associated with growth responses to drought

Applied to the dendrophenotypes of Varramista (Mazza et al., under review), the association methods VSURF, Boruta, and Tassel provides different numbers of SNPs associated with the three resilience indices assessed in extreme drought years (Table 3). VSURF identifies four SNPs, including two within our newly selected candidate adaptive genes (contig08248_183, aalba5_s000112607_28420, contig16822_456, aalba5_s00005344_59612; Table 3) related with drought responses. Boruta detects three genes, while Tassel identifies one, all of which overlap with those identified by VSURF. In addition, three specimens with a unique allelic combination for contig08248_183 (GG) and aalba5_s000112607_28420 (GG) show a significantly higher resistance and resilience than other individuals in the stand (Table S12).

4. Discussion

Since *A. alba* in Europe is generally associated with cool and moist regions at high altitudes or northern latitudes, the presence of lowland cryptic populations under warm, summer-dry Mediterranean climates may seem unexpected today. However, this finding is consistent with past *A. alba* records, showing widespread warm-loving occurrences before almost complete extirpation of these forests through land-use changes (e.g., Colombaroli et al., 2007; Martinelli et al., 2017; Tinner et al., 1999; Tinner and Lotter, 2006). This evidence suggests an ability of *A. alba* to thrive under a broader-than-expected climatic range (e.g., Vitasse et al., 2019; Walder et al., 2021). While the population genetics and evolutionary and demographic history of the sub- and meso-Mediterranean *A. alba* have been assessed (Coşgun et al., 2025), a knowledge gap remains regarding the link with the local climatic and environmental conditions. Specifically, sub- and meso-Mediterranean populations may reveal genetic peculiarities equipping them with an advantage under summer-dry, warm Mediterranean climates.

Table 3
SNPs associated with drought responses in *Abies alba* from Varramista (Rt: Resistance, Rc: Recovery, Rs: Resilience).

SNP ID	Associated drought response indices	Protein	SNP source reference
contig08248_183	Rt [v&bc], Rs [v&bc], Rc[v&bt]	PIP1 aquaporin	Roschanski et al. (2016)
aalba5_s000112607_28420	Rt [v&bc], Rs [v]	Probable protein phosphatase 2C 17	This study
contig16822_456	Rs[v&bt], Rc[v&t]	Serine/threonine protein phosphatase 2A	Roschanski et al. (2016)
aalba5_s00005344_59612	Rc[v]	DnaJ homolog subfamily B member 6 (heat shock-like protein)	This study

[v]VSURF.
[bt]Boruta tentative.
[bc]Boruta confirmed.
[t]Tassel.

4.1. Cryptic sub-Mediterranean and meso-Mediterranean populations

The discovery of Tavernelle and Poggio Antico stands in Tuscany, along with the well-known Varramista (Cortini Pedrotti, 1967; Walder et al., 2021), confirms the presence of meso-Mediterranean *A. alba* populations, that are able to compete with evergreen broadleaved *Q. ilex* and other Mediterranean species. On-site temperature data logger measurements showed that the mean July temperature reaches 25 °C at these warm sites where *A. alba* thrives and regenerates (Table S4, Supplementary material 2-Logger temperatures). Besides warm summer temperatures, these sites are also characterized by moderate amounts of precipitation (750–850 mm/year) and by summer drought, with accumulated precipitation of ~95 mm for the warmest and driest three summer months (Mazza et al., under review; Walder et al., 2021). In addition to Tuscany, the discovery of the Corcapolo lowland stand in Ticino shows that the species grows at a site characterized by 23 °C mean July temperature under more humid sub-Mediterranean conditions. Generally, the current presence of *A. alba* in Europe is associated with sites where summer temperature is between 14 and 19 °C and summer precipitation ~150–450 mm (Tinner et al., 2013). Therefore, the discovery of these lowland meso-Mediterranean and sub-Mediterranean stands confirms the capability of the species to regenerate under a wider climatic range than conventionally assumed in forest or vegetation ecology (e.g., Leuschner and Ellenberg, 2017; Mayer, 1984; Pignatti, 1998) on the basis of the environmental conditions in the today's main range of the species. Interestingly, a similar climate niche was reconstructed for the HTM, ca. 10,000–5000 years ago when meso-Mediterranean silver fir forests were wide-spread close to the shore of the Mediterranean Sea in Tuscany (with July average temperatures of ca. 24–26 °C; Colombaroli et al., 2007; Henne et al., 2013; Tinner et al., 2013; Vitasse et al., 2019), before excessive anthropogenic disturbance (e.g. fire, browsing, cutting) led to their disappearance. Similarly, in the sub-Mediterranean forelands of the Southern Alps and the Northern Apennines, summer temperatures at sites that suffered anthropogenic extirpation of silver fir forests were slightly lower, but still far warmer than today's conditions in its main range (with July average temperatures of ca. 22–24 °C; Gobet et al., 2000; Tinner et al., 2013; Vescovi et al., 2010).

Future climate projections based on the shared socioeconomic pathway 585 (SSP585; worst-case scenario) predict that by the end of the 21st century, mean July temperatures may reach 24.4 °C in Intragna in Ticino (at 1100–1250 m a.s.l., the current mean July temperature is 17–19 °C, Table 1 & Supplementary material 2) and 23.3 °C in Dürsrüti, Bern, north of the Alps (at 900 m a.s.l., the current mean July temperature is ca. 18.8 °C; Table 1). These temperatures would clearly exceed the usually supposed warmer limit of the climatic niche of *A. alba.* However, considering the warmer (and drier) climatic conditions at the Mediterranean sites (ca. 22–26 °C mean July temperature), our findings imply that the warm-adapted lineages of *A. alba* may cope well with future global warming.

4.2. Exploring population genetic structure across diverse climatic zones

SNP genotyping revealed a divergence among *A. alba* populations of Southern Italy, Tuscany, and Northern Italy/Switzerland (Ticino, Bern, Grisons), in line with the wider regional genetic structure (for European distribution, see: GENTREE, 2020) and postglacial population history (for discussion on the population structure, evolutionary and demographic history, see Coşgun et al. (2025)).

Our results suggest that patterns of genetic admixture may align with climatic variability. Despite all five populations in Tuscany—lowland or montane, planted or natural—were assigned to the same genetic cluster,

the montane population Abetone growing under cool and moist conditions showed a higher admixture with the North compared to other Tuscan populations. More strikingly, only the lowest elevation and, thus, the warmest Ticino population, Corcapolo, showed substantial admixture with Tuscany and Southern Italy, if compared to the other proximate Ticino stands growing under cooler and moister conditions at higher elevations. In fact, our on-site phenotypic observations also suggest a similarity of lowland Insubrian *A. alba* with those of Tuscany and Southern Italy, with wider and fleshier needles, strong branch production and short and squat trunks stems with many branches. These features are similar to the observations of Giacobbe (1949) on the appearance of the Mediterranean ecotype that led the author to suggest the existence of a subspecies (*Abies alba* subsp. *apennina*, see Brullo et al., 2001; Giacobbe, 1949). However, such phenotypes could also reflect phenotypic plasticity, allowing individuals to react to varying environmental conditions. The observed admixture patterns in Corcapolo and Abetone may result from a combination of historical gene flow and local adaptation to climatic conditions, highlighting the potential role of selection in shaping patterns of genetic diversity either through gene flow or local adaptation in populations growing under distinct climatic conditions.

Unlike other Tuscan populations, Poggio Antico (Tu4) showed a low level of admixture, possibly leading to it forming a separate cluster at K = 4, questioning its alignment with other regional populations. However, this tendency was not evident when we analysed the population genetic structure and evolutionary history combining our newly introduced Tuscan populations alongside the genotypes of Italian and European populations from the literature (Coşgun et al., 2025). Additionally, our previous study (Coşgun et al., 2025) revealed stronger effects of genetic drift for this site, similar to populations in the Pyrenees (genotype data from Brousseau et al. (2016)). Indeed, increased inbreeding, genetic drift, and reduced genetic diversity are observed in isolated populations, which may eventually lead to the formation of a singular STRUCTURE cluster in a scenario of strong drift and low migration. Such a scenario translates into lowered evolutionary potential to cope with environmental change and to the related risk of local extinction (Bruna, 2004; Frankham, 2005). While drought-induced diebacks in *A. alba* were already reported for the Pyrenees (Gazol et al., 2023), a high rate of tree mortality was also observed in Poggio Antico during the fieldwork. Therefore, whether these diebacks, as observed in Poggio Antico or the Pyrenees, are associated with reduced genetic diversity and, hence, adaptive potential remains to be investigated further.

4.3. Impact of environment on genetic structure

While the speciation of European trees is dating back up to millions of years ago and genetic diversity has remained largely stable over hundreds of thousands of years at least for widespread species (Milesi et al., 2024), the extant distribution of genetic lineages is strongly shaped by refugial populations during the Quaternary glacial cycles and recolonization processes (Burga and Hussendörfer, 2001; Coşgun et al., 2025; Hewitt, 1999; Liepelt et al., 2009; Piotti et al., 2017), and climate-related genetic variation is evidenced for many natural populations (Leites and Benito Garzón, 2023). Indeed, while we observed that *A. alba* populations at different elevations displayed regional genetic structure without substantial altitudinal genetic differentiation, genotype–environment association analyses revealed that a part of the genetic variation is independent from population genetic structure and related to the surrounding climate.

Combining the results from dbRDA and Gradient Forest, temperature seasonality (Bio4) comes forward as an important driving factor for the distribution of putatively adaptive genetic variation. In partial agreement, the study of Hinze et al. (2023) suggested temperature seasonality as the most important predictor of the spatial ranges of European tree species. Seasonality is an important determinant for plant phenology (e.g., flowering time and growing season; Yang et al., 2018) and plays a crucial role in the natural distribution of tree species in Europe. While the strong seasonality during the early Holocene favored rather continental taxa like deciduous *Quercus*, *Tilia*, and *P. sylvestris*, decreased seasonality in the later Holocene allowed the expansion of oceanic, frost-sensitive forest species such as *F. sylvatica* or *Q. ilex* (Huntley et al., 1989; Lang et al., 2023). In agreement, Bio4 was correlated with the genetic variation of *Quercus liaotungensis* Koidz. (Yang et al., 2018) and the distribution of *Fagus orientalis* Lipsky (Sękiewicz et al., 2022), *Pinus pinaster* Aiton (Barrio-Anta et al., 2020), and *Q. robur* (Ülker et al., 2017). Another temperature-related environmental driver suggested by dbRDA is Bio3, i.e. isothermality (ratio of diurnal variation to annual variation in temperatures). Other studies suggested it as one of the determinants of the spatial distribution of *Q. ilex* at the eastern border of the species in Türkiye (Yilmaz et al., 2024) and *P. pinaster* in Spain (Barrio-Anta et al., 2020). In line with the aforementioned literature, climatic variables related with temperature seasonality and variation are also found to be associated with the putatively adaptive genetic variation in *A. alba*.

In our analyses, most environmental variables influencing genetic variation were related to moisture, a critical factor in summer-dry Mediterranean climates. Similarly, moisture has been associated with genetic differentiation in other species and climatic regions, such as those from the summer-humid southwestern coastlands of Brazil (Silva-Arias et al., 2021). The mean monthly precipitation amount of the warmest quarter (Bio18) also comes forward as a significant environmental driver of the genetic variation in *A. alba*. Water stress affects plant metabolism through its impact on transpiration, photosynthesis, respiration, cell growth, hormone regulation, and several other physiological processes (Hsiao, 1973), and also suppresses stomatal opening to control leaf temperature under heat stress, leading to high respiration with low photosynthesis (Mittler, 2006). Accordingly, summer drought is one of the strongest limiting factors for plant growth and survival in the Mediterranean (Solé-Medina et al., 2022) and other summer-dry terrestrial biomes. The observed associations between genetic variation and bioclimatic parameters such as temperature seasonality (Bio4) and summer precipitation (Bio18) in our data likely reflect underlying physiological mechanisms, such as the regulation of transpiration and photosynthesis under varying moisture availability. These processes are critical for maintaining water balance and metabolic activity, particularly in Mediterranean environments where summer droughts impose significant stress. Intriguingly, while Bio18 (mean monthly precipitation amount of the warmest quarter) has only a moderate—although statistically significant—effect according to dbRDA with down-scaled CHELSA climate data, it becomes the most important environmental driver when meteorological station data are included. Since drought is a potential driver of the observed diebacks in lowland Mediterranean *A. alba* stands we studied, this climatic refinement reveals the importance of local measurements to achieve more precise outcomes in climate impact studies.

The annual range of monthly near-surface relative humidity (HURS range) and mean daily mean air temperatures of the wettest quarter (Bio8) were found as important factors shaping the putatively adaptive genetic variation of *A. alba* by both dbRDA and Gradient Forest. In addition, precipitation seasonality (Bio15) and mean daily mean air temperatures of the driest quarter (Bio9) were selected by one of these methods. The driest season in Southern Switzerland and Northern Italy is winter, the rest of Italy is characterized by a Mediterranean, i.e., summer-dry climate. Accordingly, Bio8 and Bio9 are drastically changing in Southern Switzerland and Northern Italy vs. Central and Southern Italy (Fig. S4). Therefore, we can attribute the significance of Bio 8 and 9 to dry vs. humid summers. In agreement, Postolache et al. (2021) revealed the importance of the precipitation–seasonal temperature associations as driving the patterns of genetic variation of *F. sylvatica*, while García-García et al. (2023) reported the genetic association of *A. alba* with precipitation seasonality. Moreover, while Meger et al. (2024) found some significant genetic associations with

Bio8 for *Q. robur*, Lu et al. (2019) identified Bio8 as one of the important climatic variables for the genetic variation of *Pinus taeda* L., along with Bio4 and Bio9. Soil water balance and available water capacity in our analyses were also selected by dbRDA for the macro- and microclimate datasets, respectively. Soil available water capacity has a profound effect on tree growth during drought (Csilléry et al., 2020; Gadermaier et al., 2024) and buffers the negative effects of water stress (Walder et al., 2021), especially considering the deep root system of *A. alba* (Martínez-Sancho et al., 2021). Some other moisture-related environmental variables (e.g., climate moisture index, growing season precipitation, precipitation seasonality) were also identified as important drivers of genetic variation.

We performed an additional dbRDA for Tuscany to pinpoint to environmental drivers of genetic variation over a wide climatic range of the same genetic lineage. This analysis revealed soil water balance, temperature seasonality, precipitation seasonality, mean monthly precipitation amount of the coldest quarter, the annual range of monthly near-surface relative humidity, isothermality, nutrient availability and soil reaction as significant environmental drivers. As suggested by Walder et al. (2021), warm late autumn seasons in the lowlands of Tuscany may buffer against the negative effects of summer drought through a prolonged or reactivated photosynthetic activity and the accumulation of carbon as observed for other evergreen species such as *Q. ilex* (La Mantia et al., 2003). Another important environmental driver for putatively adaptive variation in Tuscan *A. alba* was soil reaction (pH). The species can tolerate soils with a pH from acid to neutral (Mauri et al., 2016). However, increased acidity might be disadvantageous for *A. alba* most probably due to the leaching of some base cations and suppressing of the development of fine roots and/or mineralization (González de Andrés et al., 2022). With our microclimatic dataset, AWC explained the highest percentage of genetic variation. Although the soil water capacity, along with other soil properties, is critical for trees, there are only a limited number of studies that examine genotype–environment associations involving soil variables (see Pluess et al., 2016; Rellstab et al., 2016). We observed high tree mortality in study sites with low soil moisture availability, in slopes of Varramista (Tu1), Tavernelle (Tu2) and Poggio Antico (Tu4), suggesting that these meso-Mediterranean populations are becoming threatened by recent global warming impacts, especially by drought (Merlin et al., 2018). Walder et al. (2021) also emphasized the importance of soil water holding capacity for the ability of *A. alba* to thrive under dry climates, while Henne et al. (2015) projected the presence of *A. alba* in lowland Tuscany where soil depth is sufficient or moisture availability high (e.g. north-facing slopes). Soil depth and water holding capacity are similar for Tavernelle and Poggio Antico, but *A. alba* is experiencing a more severe dieback in Poggio Antico, also compared to the warmest and driest site Varramista, where soils are deeper and thus have higher water holding capacities. Although several adult trees died due to drought at Poggio Antico, numerous regenerating seedlings can still be observed in this area. Findings in the literature suggest that seedlings can cope with water resistance by altering leaf-to-sapwood ratios and allocating resources in the root system (Cregg and Zhang, 2001; Csilléry et al., 2020; Gehring et al., 2016). The study of Csilléry et al. (2020) revealed the tendency of *A. alba* populations from dry origins to grow smaller under drought stress, which is also consistent with the phenotypic observations in Tuscany and Corcapolo. Thus, although the potential for adaptation in Poggio Antico appears limited due to the reduced genetic diversity, we may still be witnessing the effects of natural selection.

4.4. Loci linked to climatic factors and candidate adaptive genes to climatic stress

Drought stress has a significant impact on plant growth and survival by inhibition of photosynthesis and cell growth, alteration of metabolism, accumulation of reactive oxygen species (ROS), and by leading to physio-morphological changes at the cellular level, such as stomatal closure and cellular respiration activation (Mehari et al., 2022; Vargas-Ortiz et al., 2021). Heat stress also threatens plant growth and development by reducing photosynthetic efficiency, causing oxidative damage and cell membrane dysfunction, eventually leading to dehydration (Zhao et al., 2020).

Our analyses reveal that sufficient moisture is an essential factor for shaping the adaptive genetic variation found in *A. alba.* We identified SNP variation in several genes linked with climatic stress factors using RDA and BayeScEnv, which was associated with environmental variables as proxies for limited water availability (Table 2). RDA identifies linear associations between genetic variation and environmental variables, while BayeScEnv employs a probabilistic approach that also accounts for population structure; therefore, differences in the significantly associated SNPs by these two analyses might arise from the spatial population distribution and accompanying geographically correlated climatic variables.

Our findings suggest links of ATP-dependent Clp protease proteolytic subunit-related protein (contig14580_627 & contig14580_865) and stromal 70 kda heat shock-related chloroplastic-like protein (contig00716_144) with relative humidity range, temperature seasonality and summer precipitation (Table 2). In agreement, the dendro-genomic study of Heer et al. (2018), linking variation in SNP allele frequencies and dendro-phenotypes, revealed the correlation of ATP-dependent Clp proteases (contig14580_627) and 70 kDa heat shock-related protein (contig00716_144) with the resistance and recovery of *A. alba* after drought. The PIP1 aquaporin gene is identified as correlated with relative humidity range, soil pH and drought responses (contig08248_183; Tables 2 & 3). Plasma membrane intrinsic protein (PIP) aquaporins mediate the transport of water and other small solutes across membranes (Li et al., 2014) and members of this gene family have been shown to be drought-responsive in *P. pinaster* (de María et al., 2020) and *P. taeda* (Lorenz et al., 2011) and related with drought resistance in *A. alba* (Behringer et al., 2015; Heer et al., 2018). A serine/threonine protein phosphatase 2A gene (contig16822_456; Table 2) was also correlated with relative humidity range. PP2As are essential for stress responses, plant development and hormonal regulation (Ko et al., 2023), including abscisic acid (ABA), controlling numerous developmental processes and adaptive stress responses, such as stomatal closure and modulating downstream genes (Cutler et al., 2010). Our results reveal climate association with some SNPs involved in ABA signalling. Glyceraldehyde-3-phosphate dehydrogenase b subunit (newcontig00575_232; Table 2) showed an association with relative humidity range, in agreement with the literature that it also participated in stress resistance in plants (Geng et al., 2023). In our analysis, an auxin-induced protein (a plant hormone involved in drought stress; de María et al., 2020) was also found to be related with relative humidity range (aalba5_s00278571_11484; Table 2). Another SNP we found to be associated with climate is located in contig24145_82, related with 60S ribosomal protein L7–4-like, another member of the L7 family was found to be correlated with drought resistance in *A. alba* (Heer et al., 2018). WRKY 10 (aalba5_s00068877_34157), a member of the WRKY transcription factor family, was determined to be associated with isothermality and mean daily mean air temperatures of the warmest quarter, and Lorenz et al. (2011) reported the upregulation of WRKY genes in the root transcriptome of *P. taeda* after drought stress. Additionally, phospho-2-dehydro-3-deoxyheptonate aldolase (newcontig08206_228) is also observed to be related with mean temperatures of the wettest quarter (Bio8) and reported to contribute to drought tolerance in *Lolium multiflorum* (Pan et al., 2017). Hence, our results corroborate the notion that variation in stress-related genes aligns with differences in temperature, water availability and potential drought.

Population genetic structure and genotype–environment associations, along with our previous findings, suggest a complex adaptation history in response to climate. In the lowland Ticino stand, Corcapolo, an admixture from Tuscany and Southern Italy is evident, and low F_{ST}-values between Corcapolo and Tuscany further indicate genetic

connectivity (Coşgun et al., 2025). Examination of the geographical distribution of the allelic frequencies (Fig. S8), we can observe trends in certain loci such as contig00716_144 and newcontig00575_232, in Corcapolo similar to Tuscan and/or Southern Italian populations, suggesting shared alleles and/or admixture. However, independent distributions for some SNPs located in candidate adaptive genes, such as aalba5_s00278571_11484, indicate that adaptation to climatic stress might be more complex than either independent local adaptation or the spread of adaptive alleles. These findings indicate the possibility that drought adaptation could either have evolved independently in both Ticino and Italy or originated in Italy and spread northward to the lowlands of Ticino.

In addition to SNPs associated with climate variables derived from CHELSA or locally measured weather conditions, we also looked for SNP associations with tree-ring inferred drought responses in Varramista. The PIP1 aquaporin gene (contig08248_183) and serine/threonine protein phosphatase 2A (contig16822_456) were found to be associated also with the proxies of drought responses, along with bioclimatic factors (Table 3). Additionally, a geographic pattern of allele frequency, with a strong tendency towards one of the alternative alleles in Southern Italy, was observed for both loci (Fig. 4), consistent with the commonly observed occurrence of clinal patterns in allele frequencies in populations distributed across varying environmental conditions (Eckert et al., 2010). Moreover, probable protein phosphatase 2C 17 (aalba5_s000112607_28420) and DnaJ homolog subfamily B member 6-heat shock-like protein (aalba5_s00005344_59612) were also determined to be associated with drought response. Protein phosphatase 2C (PP2Cs) functions in the ABA signalling network (Jung et al., 2020), and DnaJ proteins play critical roles in plant growth, development, and heat stress response (Fan et al., 2017). Indeed, tree-ring inferred drought responses revealed that three individuals in Varramista with a unique allelic combination for contig08248_183 and aalba5_s000112607_28420 showed a notably higher resistance and resilience compared to other individuals in this stand (Table S12). Even though this combination also has a clear North–South trend (Fig. S7), the limited number of samples in Varramista precluded a statistical verification.

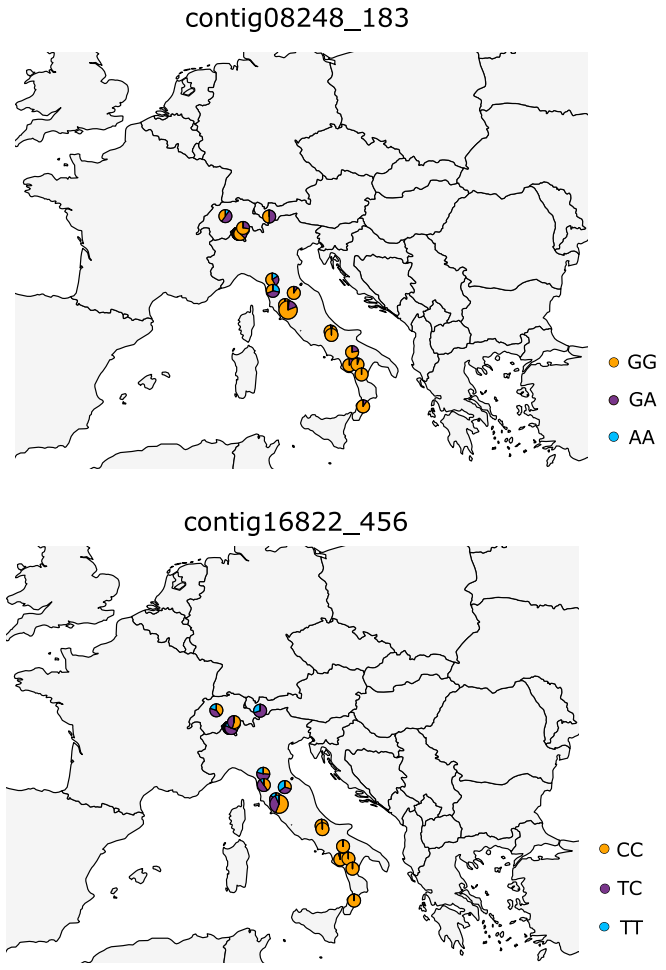

Fig. 4. Allelic distributions of contig08248_183 and contig16822_456 in *Abies alba* populations from Italy and Switzerland.

Besides the geographic patterns of allelic frequencies, we also examined age-related differentiation for the loci we regarded candidate adaptive genes (Fig. S9). Our analyses revealed notable genetic differentiation between young and adult trees across several loci, highlighting their potential roles in local adaptation to environmental changes. An increase in age-related differentiation in contig00716_144 (stromal 70 kda heat shock related chloroplastic-like) and aalba5_s00112607_28420 (probable protein phosphatase 2C 17) was observed for Swiss samples and might reflect an adaptation to varying altitudes and climatic conditions. Contig24145_82 (60S ribosomal protein l7–4-like) and newcontig08206_228 (phospho-2-dehydro-3-deoxyheptonate aldolase) showed a consistent pattern across all lineages with a high differentiation among young and adult trees, suggesting a strong directional selection, likely involving adaptive processes. Our outcomes document the interplay between selective pressures imposed by climate, such as drought and temperature extremes, which vary across regions and differently affect young and adult trees, and the physiological traits critical for survival and reproduction. These findings highlight the importance of adaptive plasticity and ongoing selection in maintaining population resilience under changing climatic conditions.

Taken together, our results emphasize the role of specific genes in the adaptive responses of *A. alba* to environmental stress, particularly to drought. The identified candidate adaptive genes not only suggest mechanisms through which *A. alba* may cope with environmental stress, particularly with limited water availability, but also offer a promising basis for future research on forest conservation and management. Understanding stress response mechanisms in *A. alba*, and other forest trees, provides insights into evolutionary strategies of woody plants to cope with challenging environmental conditions.

5. Conclusions

The discovery of *A. alba* populations from lowland sites under Mediterranean climate and their genetic links to environmental and climatic variables, alongside the populations at higher elevations, offer novel insights into the genetic variation of the species under diverse climatic conditions. Cryptic meso-Mediterranean and sub-Mediterranean lowland populations mostly align with the regional genetic structure, indicating that the species can survive in warmer and drier environments beyond its current climatic main range. This capacity might be linked to the existence of peculiar ecotypes, lineages or subspecies of *A. alba* (e.g., *A. alba* subsp. *apennina*) shaped by long-term evolutionary processes, local adaptation and gene flow. However, it remains unclear if these cryptic populations are descendants of the Holocene populations, e.g., in Tuscany and Ticino, and it needs additional research, including ancient DNA analyses of plant remains in sedimentary archives, to link Holocene and extant populations.

Our study elucidates the genetic structure of the species by adding warm-loving Mediterranean populations. Together with key environmental drivers and specific loci associated with climate and drought responses, our data reveal both, neutral demographic processes and adaptive mechanisms. These findings not only deepen our knowledge of the climatic niche of the species and climatic factors driving genetic differentiation, but also offer starting points for provenance trials, allele-specific common garden experiments and modeling research for forest management and conservation under global warming. This information contributes to the growing body of research on forest conservation under

climate change, suggesting that it is likely that certain lineages, ecotypes or subspecies have a clear advantage over others under global warming. However, it remains difficult to unambiguously infer such response patterns without further research such as common garden experiments or provenance trials. Nevertheless, given the observed link between climatic conditions, genetic properties and drought responses, we hypothesize that *A. alba* varieties from southern Europe might be particularly suited to cope with increasing heat and drought in the central European main range in the future.

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CRediT authorship contribution statement

Sevil Coşgun: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **Jérémy Gauthier:** Writing – review & editing, Methodology, Formal analysis, Conceptualization. **Giorgia Beffa:** Writing – review & editing, Investigation. **Giuliano Bonanomi:** Writing – review & editing, Investigation. **Gabriele Carraro:** Writing – review & editing, Investigation, Conceptualization. **Paolo Cherubini:** Writing – review & editing, Conceptualization. **Erika Gobet:** Writing – review & editing, Conceptualization. **Maria Leunda:** Writing – review & editing, Investigation. **Maria-Chiara Manetti:** Writing – review & editing, Methodology, Investigation. **Gianluigi Mazza:** Writing – review & editing, Methodology, Investigation. **Azzurra Pistone:** Writing – review & editing, Investigation. **Christoph Schwörer:** Writing – review & editing, Resources, Investigation, Conceptualization. **Christoph Sperisen:** Writing – review & editing, Methodology, Conceptualization. **Lieveke van Vugt:** Writing – review & editing, Investigation. **Nadir Alvarez:** Writing – review & editing, Supervision, Conceptualization. **Marco Conedera:** Writing – review & editing, Supervision, Investigation, Conceptualization. **Felix Gugerli:** Writing – review & editing, Supervision, Resources, Methodology, Conceptualization. **Willy Tinner:** Writing – review & editing, Supervision, Resources, Methodology, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data is presented in the supplementary materials. If additional data is required, please contact: sevil.cn@gmail.com

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