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# Historical translocations of silver fir in peninsular Italy: Implications for managing the genetic diversity of plantations

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ABSTRACT

Nowadays the use of forest reproductive material (FRM) is carefully regulated, but from the 18th century until few decades ago undocumented large-scale transfers of FRM has been commonly practiced in Europe. Past translocations could have had a profound impact on the genetic layout of European forests, and current plantations could either represent risks (e.g., genetic pollution for local lineages) or opportunities (e.g., unintentional assisted migration experiments in areas not covered by provenance trial networks) for extant forest genetic resources. Aiming at clarifying the role that silver fir plantations could play for the conservation of the genetic diversity of fragmented, rear-edge silver fir populations, we assembled a large genetic dataset of 3342 trees: 1553 from 48 plantations in Northern and Central Apennines, and 1789 from 38 natural populations representing possible sources of FRM. All trees were characterized with 16 microsatellite markers to reconstruct the main past translocations occurred in an area > 500 km wide in peninsular Italy. The integration of > 1000 newly genotyped individuals with previously published datasets enabled a broad review of the genetic structure of silver fir plantations across Italy. Overall, we found that ~30% of the planted individuals were translocated from a distant genetic cluster and 92% of nation-wide genetic diversity is conserved in plantations. The consequences of assessing the presence of local *vs.* non-local genotypes in plantations, as well as all downstream considerations about their spatial genetic structure and levels of genetic diversity, are discussed with a special focus on informing the management of forest tree plantations that could have high conservation value.

## 1. Introduction

Habitat loss and fragmentation are the primary causes of biodiversity decline worldwide (Haddad et al., 2015). These processes are of particular concern when they affect forests that are home to most of the world's terrestrial biodiversity (FAO, 2020). In this context, translocations (human-facilitated releases of organisms into the wild, *sensu* Menges, 2008) are a crucial tool to prevent further biodiversity loss, either by reinforcing the size and/or genetic diversity of existing small populations or establishing new self-sustaining populations (Menges, 2008; Weeks et al., 2011). The origin of the forest reproductive material (FRM) used in forest plantations and restoration programmes is of paramount importance for the survival and growth of current and future forests (Aitken and Bemmels, 2016). While nowadays the use of FRM is carefully regulated, this was not the case until few decades ago. In Europe, in the 18th century large-scale transfer and use of non-local seeds for artificial regeneration became common practices, but the origin of the FRM used remained largely undocumented (Koskela et al., 2014). Yet, these past translocations have had a profound impact on the structure, ecology and genetic layout of European forests.

Considering the growing awareness about the relevance of the genetic component of biodiversity, it is essential to discriminate between the genetic characteristics of native forest tree populations and any FRM that may have been translocated during centuries of forest management. Recent studies highlighted the eco-evolutionary risks and benefits of changing *vs.* not changing seed provenance practices under novel environmental conditions (e.g., Laikre et al., 2010; Jordan et al., 2024). The risks associated with introducing non-local FRM are particularly critical when natural populations of relatively small size exist in the surroundings of the planted stands, as genetic modifications resulting from pollen introgression could disrupt local adaptation (Laikre et al., 2010; Steinitz et al., 2011; Unger et al., 2016). On the other hand, the

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main risk of strictly relying on local FRM is related to the novel environments adult trees will likely face due to climate and land use change for which that may no longer be fit (Jordan et al., 2024). In addition, evidence is emerging that planting multi-provenance instead of single-provenance FRM could be a promising approach to increase the productivity and adaptive potential of future artificial forests (Prakash et al., 2024; Milani et al., 2026). Already established plantations could as well represent useful conservation interventions *per se* (Jia et al., 2020), or unintentional assisted migration experiments (Oggioni et al., 2024) in areas neither hosting nor providing seed sources for provenance trial networks. In this context, determining the origin of plantations, as well as quantifying their genetic variation with respect to natural populations, is crucial for assisting forest management in areas where natural populations and plantations coexist and for understanding their potential degree of adaptability to environmental changes (McKay et al., 2005; Wagner et al., 2015; Unger et al., 2016; Jansen et al., 2017; Santini et al., 2018; Jordan et al., 2019; Jia et al., 2020; Oggioni et al., 2024; Olsson et al., 2025; Kodym et al., 2026).

Silver fir (*Abies alba* Mill.) is a conifer widely distributed in central and southern Europe, showing a particularly complex genetic structure in the Italian and Balkan peninsulas (Piotti et al., 2017; Gömöry et al., 2020). In the Apennines, at mid longitude along the rear edge of the species range, the combination of climatic fluctuations and human activities has progressively reduced the role of silver fir as a dominant forest tree species over the last thousands of years and favoured the establishment of monospecific beech forests (Magri et al., 2015; Morales-Molino et al., 2021). Nowadays silver fir occurs in highly fragmented natural remnants across the Apennine chain (Rovelli et al., 1995), which often suffer the negative consequences of genetic drift induced by demographic decline (Avanzi et al., 2024). In this scenario, the massive presence of silver fir plantations in the area could either represent a reservoir of genetic diversity and facilitate pollen gene flow across fragmented natural populations, thus enhancing the ability of the species to withstand the present and future pressures of climate change, or pose serious risks of genetic dilution and outbreeding depression. A thorough understanding of the origin and levels of genetic diversity of the FRM that have been used to establish such plantations in the past is required to assess such potential advantages and disadvantages. Recent studies used molecular markers to provide the first insights into the origin of silver fir plantations within two Italian national parks in Northern and Central Apennines showing the presence, at a regional scale, of a mixture of single- and multi-provenance stands, with FRM translocated up to 1000 km away (Santini et al., 2018; Oggioni et al., 2024).

In the present work, already available genetic data were complemented with information on 28 additional plantations to reconstruct the main silver fir translocations that occurred in an area > 500 km wide in peninsular Italy, a region where silver fir has been subject to a wide variety of management regimes in the last millennium and where reafforestation actions have intensified in the last two centuries (Vazzano et al., 2011; Urbinati and Romano, 2012; Santini et al., 2018; Motta et al., 2023). Taking advantage of a reference dataset of 38 Italian natural populations, characterized with the same set of 16 microsatellite markers, the present work aims to unveil: i) how much of the genetic diversity harboured by the species at the national level is represented in the plantations, ii) the extent to which non-local FRMs have been used, and iii) the potential existence of a spatial and/or temporal pattern in the use of non-local FRM. Our findings shed new light on the role that plantations could play in the conservation of the genetic characteristics of silver fir rear-edge, fragmented populations, and to inform effective genetically-based management strategies that enhance the species' chances of facing future changes.

## 2. Materials and methods

### 2.1. Sampling and genotyping of silver fir plantations

Genetic data from 48 silver fir plantations, for a total of 1553 individuals, were used to reconstruct the main species' translocations that occurred in peninsular Italy. Out of these 48 plantations, 28 were specifically characterised for this study, whereas 20 came from previously published studies (Santini et al., 2018; Oggioni et al., 2024; Table S1). Plantations occur across three main geographic macro-areas in Northern and Central Apennines: the Tuscan-Emilian Apennines (TEA), the Tuscan-Romagnol Apennines (TRA), and the Abruzzo Apennines (ABA) (Fig. 1). Each macro-area was further subdivided into two areas, northern (–N) and southern (–S), resulting in a total of six study areas. After consulting with local forest managers, all sampling sites were carefully selected among stands classified as plantations in each investigated macro-area. Young individuals possibly generated by recent, post-plantation recruitment, were carefully avoided.

Plant material was collected from a median of 24 individuals per plantation (Table S1), each spaced at least 20 m apart to minimize the inclusion of related individuals. The Abetina Reale (ARL) plantation, located in the TEA-S area, was the only stand that was sampled more intensively (i.e., 300 individuals) due to its large size (> 300 ha) and historical evidence suggesting potential autochthony in some of the small valleys within this large, historically managed stand. Genomic DNA was extracted from approximately 30 mg of frozen needle tissue using the DNeasy 96 Plant Kit (Qiagen, Germany), following the manufacturer's protocol. All sampled individuals were genotyped at 16 unlinked nuclear microsatellite loci (NFF7, Hansen et al., 2005; Aag01, Aat01–Aat06, Aat08–Aat11, Aat13–Aat16, Postolache et al., 2014), already used for characterizing silver fir Italian populations (e.g., Piotti et al., 2017; Santini et al., 2018; Avanzi et al., 2024; Vajana et al., 2024). Fourteen loci were derived from expressed sequence tags, while two (i.e., NFF7 and Aag01) were genomic microsatellites. Details on multiplexing strategies and PCR conditions are provided in Postolache et al. (2014). PCR amplifications were performed using a GeneAmp PCR System 9700 thermal cycler (Perkin Elmer). Amplified fragments were separated on an AB 3500 capillary sequencer (Applied Biosystems, USA), using LIZ-500 as an internal size standard. Allele sizing was carried out manually with GeneMarker software (SoftGenetics).

### 2.2. Data analysis

Standard within-population genetic diversity parameters (number of alleles, *Na*; observed and expected heterozygosity, $H_O$ and $H_E$; fixation index, $F_{IS}$) were calculated using GenAlEx (Peakall and Smouse, 2012) for all silver fir natural populations and plantations. Allelic richness (*Ar*) values were estimated by using HP-RARE (Kalinowski, 2005), rarefying samples to 34 gene copies. The number of private alleles (i.e., alleles exclusively found in a single stand) was calculated to specifically evaluate the amount of genetic diversity embedded in plantations but absent from natural populations. Differences in genetic diversity parameters between natural populations and plantations were assessed using Welch's *t*-tests. Comparisons were performed at two geographic levels: i) between all plantations and all natural populations, and ii) between all plantations of a specific macro-area and the nearby natural populations. All analyses were done in R environment (R Core Team, 2025).

A reference dataset comprising 38 silver fir natural populations, covering the extant genetic diversity of the species in Italy, was used to reconstruct the genetic cluster of origin of plantations. This dataset included 36 populations previously characterized with the same 16 microsatellite markers (Vajana et al., 2024), and two additional populations specifically genotyped for this study (i.e., VIV and FIO; Table S1). A preliminary assessment of the genetic structure of natural populations was conducted using the Bayesian clustering algorithm implemented in STRUCTURE v2.3 (Pritchard et al., 2000). STRUCTURE

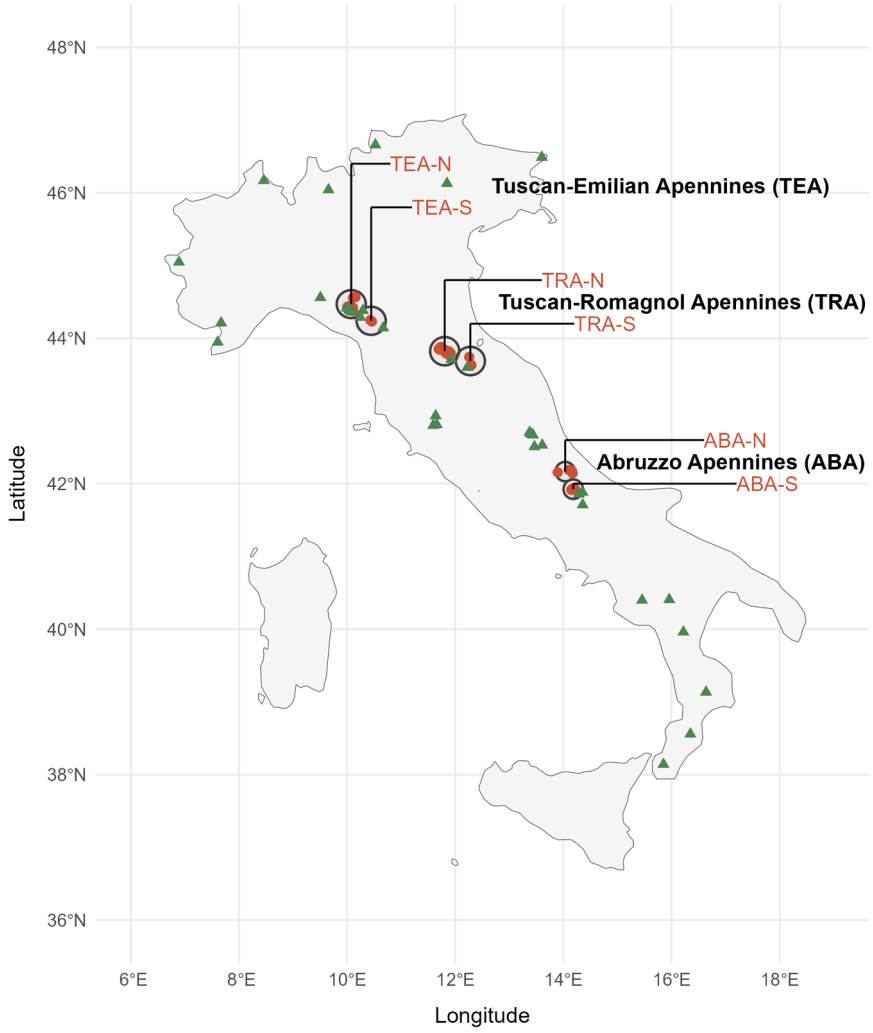



**Fig. 1.** Distribution of silver fir plantations investigated in the present study. Plantations (red dots) are grouped into three macro-areas (i.e., TEA, TRA, ABA), each subdivided into two areas, northern (-N) and southern (-S). The green triangles show the natural populations that were used as references to reconstruct the genetic cluster of origin of plantations.

was run using an admixture model and correlated allele frequencies (Falush et al., 2003), and with no prior on sampling locations. The most likely number of genetic clusters ($K$) was assessed by testing values ranging from one to ten, with 20 independent replicates per each $K$. Each run consisted of a burn-in period of $1 \times 10^4$ iterations followed by $5 \times 10^4$ iterations for parameter estimation. Replicated runs for each $K$ were aligned and averaged using CLUMPAK (Kopelman et al., 2015). The optimal number of $K$ was determined based on both Evanno et al. (2005)'s $\Delta K$ statistic and the log-likelihood trend across the tested scenarios. In addition, a hierarchical AMOVA (Excoffier et al., 1992) was performed in GenAlEx for each Bayesian clustering solution (i.e., $K$ from two to ten) to evaluate the trend in the amount of molecular variance explained by differences among genetic clusters ($F_{RT}$) across $K$ values. Once the optimal clustering solution was selected, only individuals showing a probability > 80% to belong to one of the identified genetic clusters were retained for subsequent analyses. The genetic structure of natural populations was further evaluated through a Principal Coordinates Analysis (PCoA) on the matrix of pairwise distances among populations, to provide an independent validation of the Bayesian clustering results. The PCoA was carried out by using Smouse and Peakall (1999)'s genetic distance within GenAlEx.

The subset of individuals belonging to the identified genetic clusters with a probability > 80% was used as a 'training' dataset to carry out an assignment test of the planted trees using GeneClass2 (Piry et al., 2004). The assignment test was performed using the Rannala and Mountain (1997)'s Bayesian approach, with a 0.05 significance threshold. Individuals were considered reliably assigned to one of the identified genetic clusters only when their individual membership probability exceeded 80%, otherwise they were considered 'not assigned'.

Planted trees, together with individuals in the 'training' dataset, were also included in a second PCoA, performed at the individual level. This analysis was designed to provide a qualitative and visual representation of how planted trees were distributed within the reduced coordinate space with respect to the genetic clusters used as a reference.

### 2.3. Additional analyses in two areas with a documented, long-lasting history of forest management

To investigate the potential presence of spatial and/or temporal patterns in the use of FRM of different origin, additional specific analyses were conducted on (i) the Abetina Reale plantation (ARL) and (ii) on the plantations located in the Casentino Forests (all stands in the TRA-N area, Table S1). The former is the largest silver fir stand in the Northern Apennines, an area where natural populations of the species are extremely scattered and reduced in size (Avanzi et al., 2024). It spans more than 300 ha of almost pure silver fir forest and over 500 years of management history for timber production (Schwarz, 2020). The latter are in an area where silver fir has a millenary history of management,

generating what is considered the oldest silviculture treaty (Urbinati and Romano, 2012; Motta et al., 2023). Furthermore, historical evidence suggests that the species was extensively translocated from Bohemia at the beginning of the 19th century to recover from the extensive logging of the previous century (Sabbatini, 1987; Hofmann and Perulli, 2000; Agostini and Alberti, 2018).

To assess the presence of FRM of Bohemian origin within TRA-N plantations, an assignment test was run by assembling a specific 'training' dataset as follows. Using the same settings described above, STRUCTURE was run on data from the two natural populations that represent the possible origins of the FRM used: a local natural population occurring in the area (i.e., La Verna, LVE), and a Bohemian population from the Šumava mountains (i.e., SUM), previously characterized by Santini et al. (2018). STRUCTURE was run only at K = 2, and individuals showing a probability > 80% to belong to one of the two genetic clusters (i.e., local *vs.* Bohemian) were retained in the 'training' dataset. After having removed trees that were not previously assigned to the regional reference cluster (see Results), an assignment test was performed on the remaining individuals using GeneClass2 to distinguish planted trees of local or Bohemian origin. Trees were considered reliably assigned to one of the two genetic clusters only when the probability exceeded 80%, otherwise they were considered 'not assigned'.

In both ARL and TRA-N plantations, the potential existence of temporal trends in the use of FRM of different origin was evaluated using tree size (i.e., DBH) as a proxy of age. DBH is not a precise estimator of individual tree age, in particular for shade-tolerant species in natural conditions. However, the analysis of such relationship in a subset of 280 trees from TRA-N, for which the plantation year was available, showed a significant positive correlation between DBH and plantation year (Pearson's r = 0.645, $p < 0.001$), supporting its use as an approximate indicator of age within predominantly even-aged plantations. Differences in DBH among planted individuals assigned to different genetic clusters were assessed using a non-parametric Kruskal-Wallis test followed, when necessary, by Dunn's post-hoc pairwise comparisons with Bonferroni correction for multiple testing. In ARL, analyses were performed only on individuals with > 80% probability of belonging to the identified genetic clusters. For TRA-N, analyses were performed by comparing three groups: i) trees assigned to the local genetic cluster, ii) trees assigned to the Bohemian cluster and iii) 'not assigned' trees potentially reflecting hybrid ancestry. Spatial autocorrelation in both individual assignments to the identified genetic clusters and DBH was assessed using join-count tests and Moran's I, respectively. Spatial autocorrelation of Moran's I was selected over more refined 2-D methods to use the same approach over plantations necessarily sampled with different spatial schemes. Statistical significance was evaluated using permutation tests. All analyses were performed in the R environment.

## 3. Results

### 3.1. Levels of genetic diversity in silver fir plantations vs. natural populations

All microsatellite markers were polymorphic, with a total and mean number of alleles of 153 and 9.56 (ranging from two alleles at Aat16 to 33 at NFF7), respectively. Overall, 12 and eight private alleles were detected in natural populations and plantations, respectively. This indicates that, in terms of allelic composition, 7.8% of the observed allelic diversity was private to natural populations, while 5.2% was private to plantations. Genetic diversity parameters for all natural populations and plantations are reported in Table S1. No significant differences were observed for any genetic parameter when comparing all natural populations to all plantations. Nonetheless, differences emerged when the comparisons were made between all plantations of a given macro-area and the nearby natural populations. In TEA, where NER, ORS, SCL, RPM, PIA, LAG, BAL, VEN, CER and ABE were defined as the nearby natural populations, plantations showed significantly higher allelic richness ($t$ = -2.58, df = 21.93, $p = 0.017$) and marginally significant higher expected heterozygosity values ($t$ = -1.99, df = 16.94, $p = 0.063$) than nearby natural populations. In TRA, where LVE and BTR were defined as the nearby natural populations, allelic richness ($t$ = -4.30, df = 23.92, $p < 0.001$) and expected heterozygosity ($t$ = -2.19, df = 23.99, $p = 0.038$) were both significantly higher in plantations than in nearby natural populations. Finally, in ABA-S, where ABS, CME, and RSL were defined as the nearby natural populations, plantations had significantly higher expected heterozygosity ($t$ = -2.65, df = 4.80, $p = 0.047$), as well as marginally significant higher allelic richness ($t$ = -2.39, df = 4.84, $p = 0.064$) and observed heterozygosity ($t$ = -2.08, df = 4.51, $p = 0.098$) than nearby natural populations.

### 3.2. Definition of reference genetic clusters for assignment tests

Based on $\Delta K$ statistic, Bayesian clustering identified $K = 2$ as the optimal clustering solution, separating populations located north and south of the Gran Sasso and Majella massifs along the Apennines (Fig. 2a, S1, and S2). This primary genetic split was also supported by AMOVA results (Fig. S3), which showed the highest among-group genetic differentiation at $K = 2$ ($F_{RT} = 0.079$, $p < 0.001$). Beyond this point, $F_{RT}$ decreased sharply and stabilized between 0.056 and 0.061, indicating that higher $K$ values did not reveal further significant genetic sub-structures. Although the $\Delta K$ statistic supported $K = 2$, the mean log-likelihood continued to increase with $K$, reaching its maximum at $K = 10$ but beginning to stabilize from $K = 4$ onwards. Among alternative clustering solutions, $K = 4$ was chosen as a biologically meaningful representation of population genetic structure for tracing past translocations of the species in Italy. At this hierarchical level, four geographically coherent genetic clusters emerged (Fig. 2b): two main clusters, one including Northern Apennines and Eastern Alps (NAPP; in blue) and one comprising southern populations up to the latitude of Gran Sasso and Majella massifs (SAPP; in red), and two more geographically limited clusters in the Central Apennines (CAPP; in yellow) and the Western Alps (WALP; in green) (see also Fig. S2).

Principal Coordinates Analysis (PCoA) supported the results obtained by Bayesian clustering. The first axis primarily separated SAPP populations from all other genetic clusters, reflecting the major north-south genetic differentiation detected at $K = 2$ (Fig. 2c), while the second axis distinguished WALP populations from those belonging to the NAPP and CAPP genetic clusters (Fig. 2d). The two axes, which together explained almost 60% of the total variance, supported the distinctiveness of the four genetic clusters identified at $K = 4$.

### 3.3. Assignment of planted individuals to the four identified genetic clusters

Individuals showing strong membership (> 80%) to one of the genetic clusters identified at $K = 4$ constituted the reference for the subsequent assignment test. A total of 1041 individuals met this criterion (i.e., 223 belonged to WALP, 200 to NAPP, 218 to CAPP and 400 to SAPP) and were included in the 'training' dataset.

Overall, 1140 out of 1553 planted individuals (73.4%) were assigned to one of the four genetic clusters with a probability > 80%. Of the assigned individuals, 574 (50.3%) belonged to the NAPP genetic cluster, 270 (23.7%) to SAPP, 199 (17.5%) to WALP, and 97 (8.5%) to CAPP (Fig. 3a, Table S2).

To assess which seed sources were used to establish the plantations under study, it was first necessary to define a regional genetic reference for each macro-area. Such choice was challenging because natural silver fir populations showed high levels of genetic admixture and gradual transitions among genetic clusters, especially in Central Alps and Northern and Central Apennines. Therefore, for interpreting assignment results, we considered the predominant genetic cluster in each macro-area at $K = 4$ (Fig. 2b) as the regional reference cluster. NAPP was

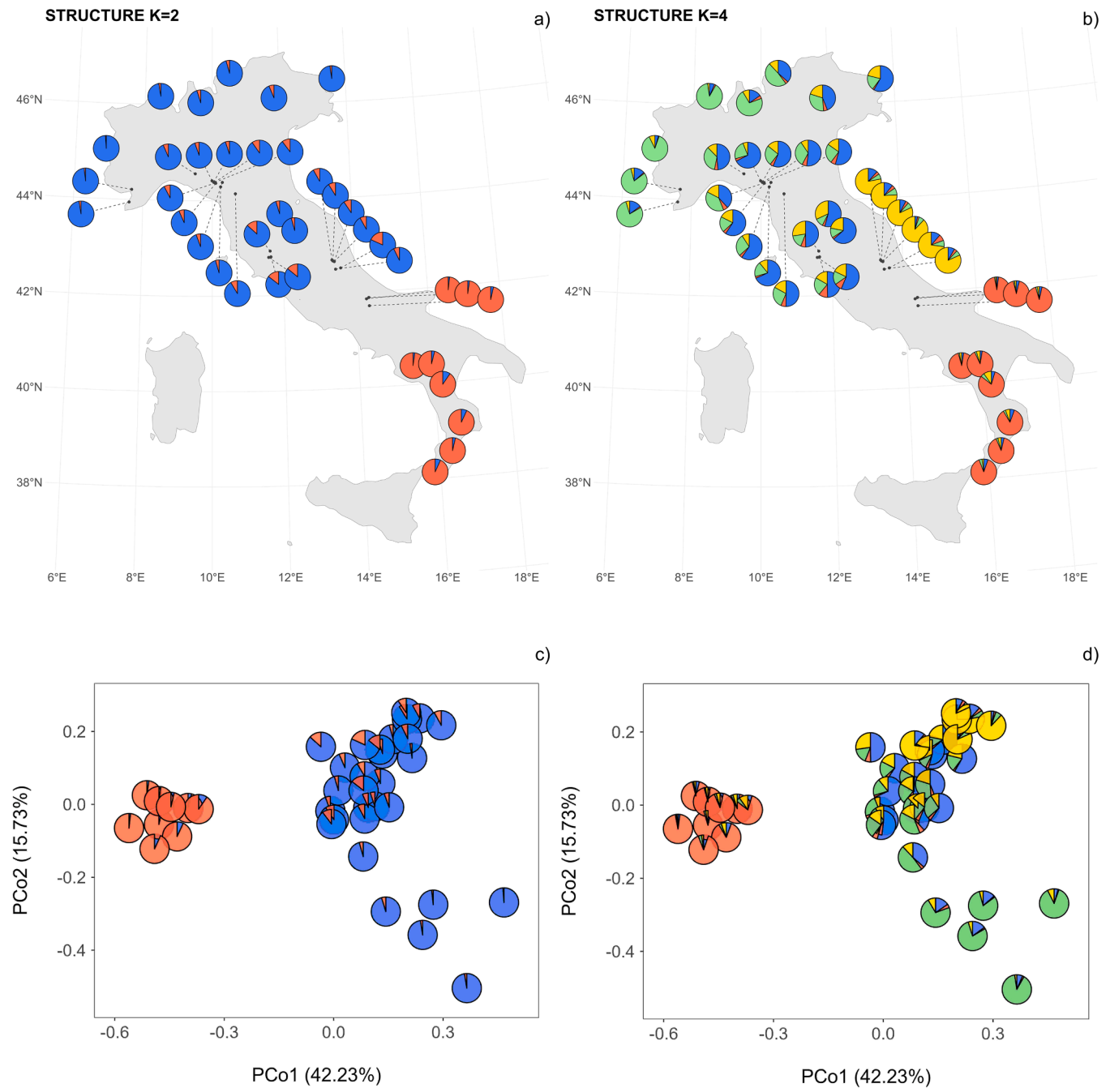



**Fig. 2.** Bayesian clustering analysis and Principal Coordinates Analysis (PCoA) of silver fir natural populations. Average ancestry proportions were shown for each population for $K = 2$ (a, c) and $K = 4$ (b, d). Pie charts colours refer to the main genetic clusters to which populations were assigned: Western Alps in green, Northern Apennines and Eastern Alps in blue, Central Apennines in yellow, Southern Apennines in red (see Fig. S2 for individual q-values).

therefore considered the regional reference cluster for both TEA and TRA, while SAPP was considered the regional reference cluster in the ABA-S area. This classification does not imply that macro-areas were exclusively composed of a single genetic cluster but rather identifies the genetic component that is most characteristic of each region. This choice allowed us to depict general translocation trends that would have been impossible to describe if we had assigned each planted tree to each natural population, the only possible alternative to properly account for admixture. No regional reference cluster was identified for ABA-N because its geographic location is at similar distance from natural populations belonging to different genetic clusters.

Since forest genetic resources in Italy have traditionally been managed at the regional level, assignment test results and subsequent analyses are presented separately for each area, to provide a more meaningful framework for interpreting translocation patterns.

### 3.3.1. *Tuscan-Emilian Apennines (TEA)*

Within the area located in the northern part of TEA (TEA-N), the origin of the 12 plantations was highly heterogeneous (Fig. 3a,b, Table S2). Among all planted individuals, 77.7% could be confidently assigned to one of the four genetic cluster, while 22.3% could not. In particular, 29.5% were assigned to the regional reference cluster NAPP, 21.9% to SAPP, 21.9% to WALP, and 4.5% to CAPP (Fig. 3a, Table S2). Considering only assigned individuals, three plantations showed a large majority of individuals assigned to NAPP (BAR, PCR, and TIC). In contrast, seven plantations were mostly assigned to other genetic

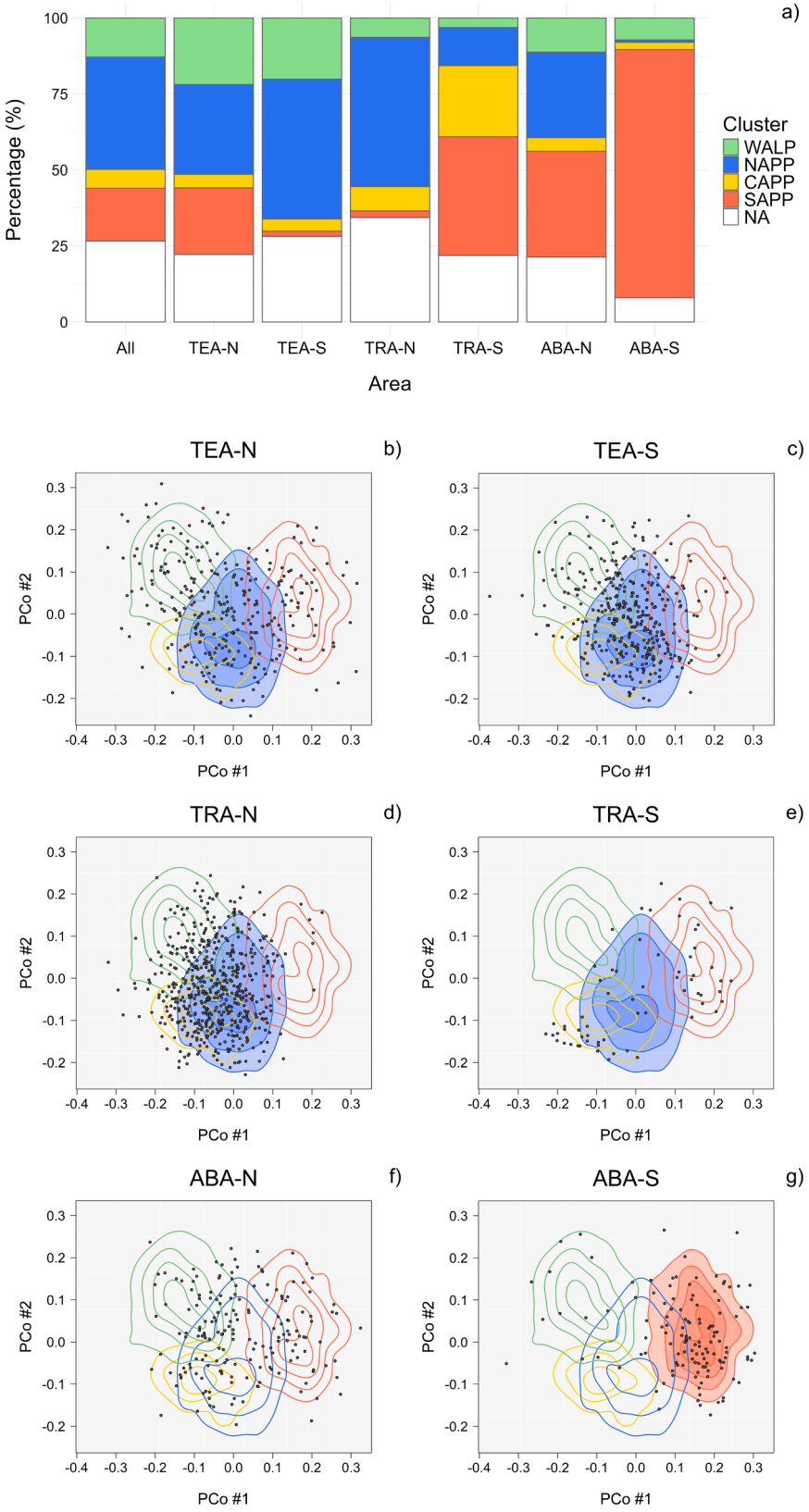



**Fig. 3.** a) Percentage of individuals assigned to one of the four genetic clusters (i.e., Western Alps in green, Northern Apennines and Eastern Alps in blue, Central Apennines in yellow, Southern Apennines in red) with a probability > 80% or, conversely, not assigned to any genetic cluster (in white), for each area. b-g) Results of the Principal Coordinate Analysis at the individual level for each area. Planted individuals are represented by black dots. Reference individuals of the 'training' dataset are not shown directly, but through kernel density distributions estimated with the *kde2d* function of the R package MASS (Venables and Ripley, 2002). The expected regional reference cluster (i.e., NAPP for TEA-N, TEA-S, TRA-N, TRA-S; SAPP for ABA-S; no expectation for ABA-N) is represented by filled contour lines.

clusters: two of WALP origin (GUP and LGD) and five of SAPP origin (CIR, FRG, MNT, PBA, and POG) (Fig. S4, Table S3). Of the eight private alleles found in plantations, four were in TEA-N. Interestingly, a single plantation (FRG) harbored three private alleles, while the fourth was found in CIR.

Further south within TEA, the two plantations located in the TEA-S area (ARL and GIO) were predominantly assigned (46%) to the regional reference cluster NAPP, while 20.1% of individuals were assigned to the WALP genetic cluster. Notably, 28.2% of individuals could not be confidently assigned to any genetic cluster with a probability $>80\%$ (Fig. 3a,c; Table S2). Considering only assigned individuals, ARL and GIO resulted to be very similar in terms of genetic cluster composition (Fig. S4 and Table S3). Despite the large number of individuals characterized in ARL, no private allele was detected in the two plantations.

### 3.3.2. *Tuscan-Romagnol Apennines (TRA)*

In TRA-N, 65.6% of planted individuals could be confidently assigned to one of the four genetic cluster, with 49.1% of them belonging to the regional reference cluster NAPP, indicating a putatively prevalent use of local material (Fig. 3a,d and Table S2). Considering only assigned individuals, three plantations (CAR, ERE, and QUA) exhibited up to 38% of individuals assigned to WALP, while in one plantation (OIA) 25% of individuals were assigned to SAPP (Table S3 and Fig. S4).No private alleles were detected in any of the TRA-N plantations.

Further south within TRA, only 12.5% of individuals of the two plantations located in the TRA-S area were assigned to the regional reference cluster NAPP. Most individuals were assigned to SAPP and CAPP (39.1% and 23.4%, respectively), indicating a likely predominant use of non-local material (Fig. 3a,e and Table S2). These proportions are markedly different in the two plantations: PMA was mainly composed of individuals assigned to SAPP (86%), whereas MMV by individuals assigned to CAPP (67%) (Table S3 and Fig. S4). One individual carrying an allele private to plantations was detected in PMA.

### 3.3.3. *Abruzzo Apennines (ABA)*

Most ABA-N individuals were assigned to the SAPP (34.8%) and NAPP (28.1%) genetic clusters, while the remaining individuals were assigned to WALP (11.2%) and CAPP (4.5%). Overall, 21.3% of individuals could not be assigned with high confidence to any of the four genetic clusters (Fig. 3a and Table S2). Unlike other study areas, the regional reference cluster could not be clearly identified in ABA-N

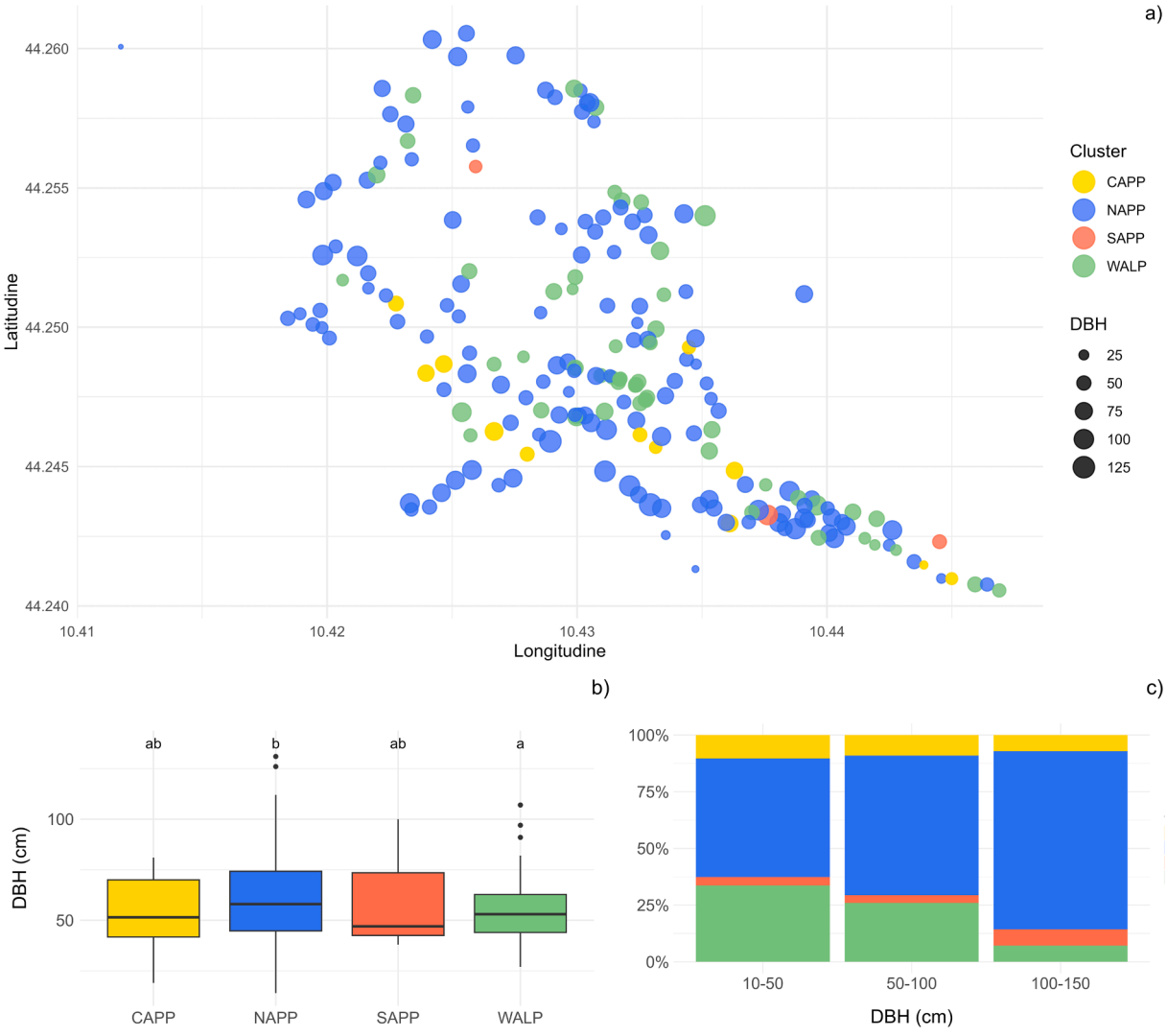



**Fig. 4.** Results of the additional analyses performed for the Abetina Reale (ARL) plantation. (a) Spatial distribution of the individual assigned to the four genetic clusters (i.e., Western Alps in green, Northern Apennines and Eastern Alps in blue, Central Apennines in yellow, Southern Apennines in red), with point size proportional to DBH classes. (b) Distributions of DBH values of individuals assigned to the four genetic clusters, with letters indicating significant differences according to the post-hoc Dunn test, after Bonferroni correction. (c) Percentage of individuals assigned to the four genetic clusters across DBH classes.

(Fig. 3f). In general, a highly heterogenous origin of plantations was found in this area. Two plantations were mostly made of trees of NAPP origin, one plantation was mostly of WALP origin and one of SAPP origin. The last stand, FOS, is a mixed-origin plantation with a similar prevalence of individuals assigned to SAPP and NAPP (Table S3 and Fig. S4). In the latter plantation, two private alleles were detected.

Further south in ABA, plantations within ABA-S were mainly composed of individuals assigned to regional reference cluster SAPP (81.6%), indicating a largely prevalent use of local material. Only 8% of individuals could not be assigned with high confidence to any of the genetic clusters (Fig. 3a,g and Table S2). At the plantation level, the only plantation that did not follow this general trend was PPI, where 50% of individuals were mainly assigned to WALP (Table S3 and Fig. S4). Two private alleles were detected in the CAS plantation.

### 3.4. Genetic and spatial patterns in two areas with a documented, long-lasting history of forest management

Spatial autocorrelation analysis in the large and historically-managed ARL plantation revealed a clear spatial structure in DBH (Moran's I = 0.177, $p < 0.001$), indicating that trees with similar size were spatially clustered (Fig. 4a). Join-count tests revealed significant spatial aggregation for the WALP genetic cluster (Fig. 4a). In addition, DBH was significantly different among the four genetic clusters ($\chi^2 = 11.63$, df = 3, $p = 0.009$). In particular, post-hoc Dunn tests revealed a significant difference between the DBH of individuals assigned to NAPP and WALP (adjusted $p = 0.006$), whereas all other pairwise comparisons were not significant (Fig. 4b). Consistently, NAPP individuals were predominantly represented in the larger DBH classes (i.e, 50–100 and 100–150 cm), while WALP individuals were mainly concentrated in the

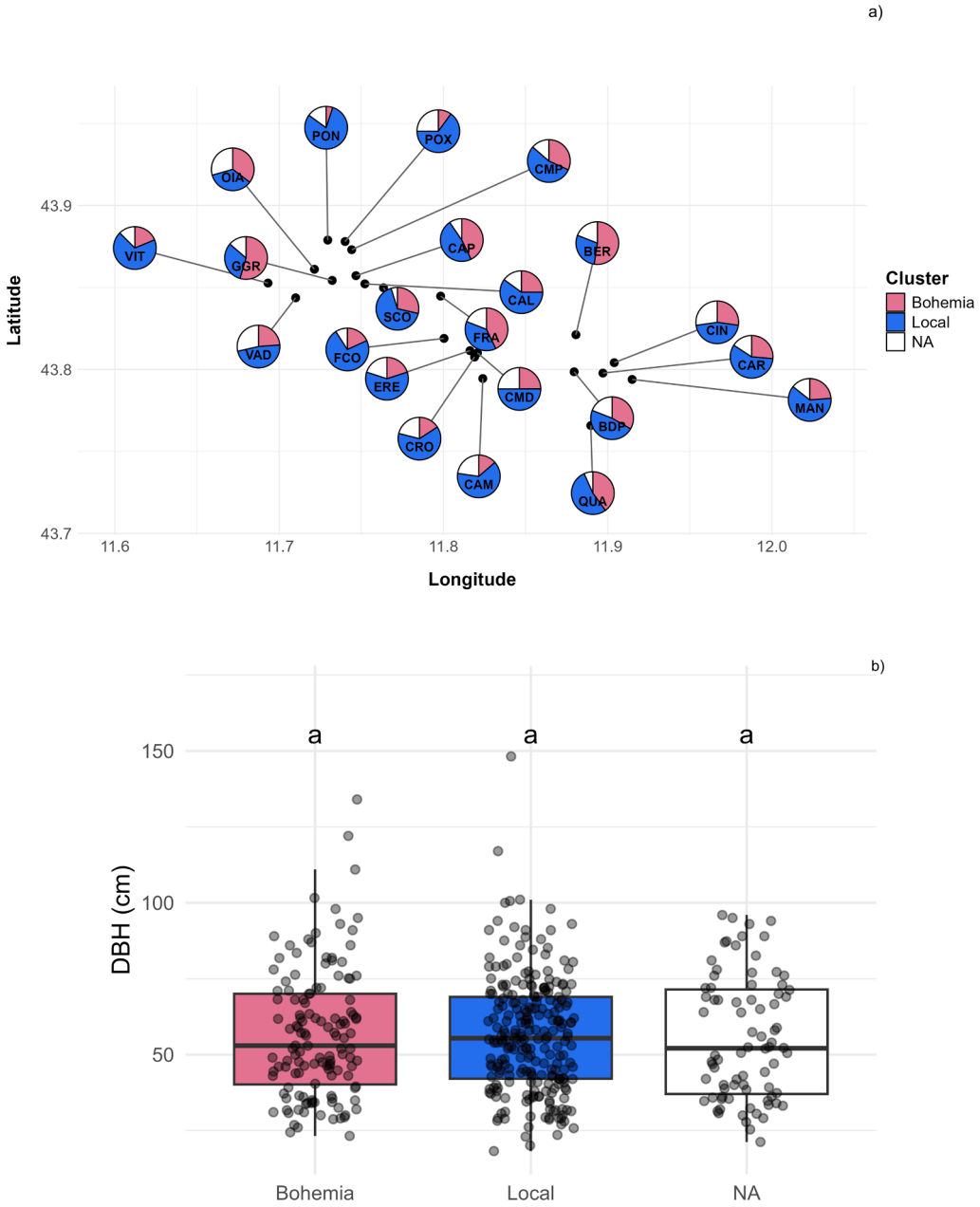



**Fig. 5.** Results of the additional analyses performed for TRA-N plantations. a) Plantation-level proportions of individuals assigned to the Bohemian genetic cluster (in violet), local genetic cluster (in blue), or not assigned (in white). b) Distributions of DBH values of individuals assigned to local and Bohemian genetic clusters, or not assigned, with letters indicating significant differences according to the post-hoc Dunn test.

smallest class (10–50 cm). Individuals assigned to CAPP and SAPP were similarly distributed across DBH classes (Fig. 4c).

To assess the presence of Bohemian FRM in TRA-N, an area where Bohemia could have represented a preferential origin of FRM in 19th century extensive reforestation programs in the area, a second assignment test was carried out on 459 individuals assigned to the regional reference cluster NAPP or not assigned in the first assignment test (see Paragraph 3.3.2). Among these, 53.6% were assigned to the local genetic cluster, 28.8% were assigned to the Bohemian genetic cluster, and 17.6% were not assigned. At the plantation level, the proportion of individuals of Bohemian origin ranged from 5% in PON to 55% in GGR (Table S3 and Fig. 5a).

A clear spatial structure in DBH was found in TRA-N (Moran's I = 0.407, $p < 0.001$; Fig. S5). In contrast, join-count tests indicated that genetic clusters were randomly distributed across TRA-N plantations, with no significant spatial aggregation at the area level (Fig. S5). No significant differences in DBH were detected among the three genetic groups (i.e., local, Bohemian, and not assigned trees; $\chi^2 = 0.35$, df = 2, $p = 0.841$) (Fig. 5b).

## 4. Discussion

The integration of > 1000 newly genotyped individuals with previously published datasets enabled a broad review of the genetic structure of silver fir plantations across Italy. Bayesian clustering and multivariate analyses consistently recovered the main phylogeographic patterns previously described for Italian silver fir natural populations, with a clear genetic differentiation among Northern, Central, and Southern Apennines populations (Piotti et al., 2017; Santini et al., 2018), as well as the distinctiveness of Western Alpine populations (Oggioni et al., 2024). Based on such a dense and discriminant reference dataset, which provided a robust empirical basis for reconstructing the main historical translocations that fueled the silver fir plantations in the Northern and Central Apennines, 73% of the 1553 planted individuals analyzed were assigned with high confidence to their genetic cluster of origin. Where the expected regional reference clusters were NAPP (i.e., TEA and TRA) and SAPP (i.e., ABA-S), approximately 30% and 10% of the planted individuals, respectively, were found to be translocated from a distant genetic cluster. The consequences of assessing the presence of local *vs*. non-local genotypes in plantations, as well as all downstream considerations about their spatial genetic structure and levels of genetic diversity, are discussed with a special focus on informing the management of forest tree plantations that could have high conservation value.

### 4.1. Historical translocations of silver fir and conservation value of plantations

Across the study areas encompassing the Northern and Central Apennines, plantations showed a highly variable genetic composition, reflecting heterogeneous reforestation histories. Plantations located within the geographic range of a given genetic cluster were not necessarily composed of genetically local material, highlighting that geographic proximity alone does not implies that only local seed sources were used in peninsular Italy. In both the Tuscan-Emilian and Tuscan-Romagnol Apennines (TEA and TRA), the NAPP genetic cluster, identified at $K = 4$ as the regional reference cluster, was dominant in most sampled plantations, indicating more localized seed sourcing and stronger continuity with natural populations. However, the recurrent detection of the WALP genetic cluster in TEA, the high proportion of individuals from SAPP in TEA-N, as well as the prevalence of SAPP and CAPP in the TRA-S area, provide robust evidence that local seed sources were often integrated with multiple and geographically distant ones. As already found in the Alpine region and, more generally, in Central Europe (Wagner et al., 2015; Jansen and Geburek, 2016; Jansen et al., 2017), reforestation practices in these areas were not strictly limited to local provenances and likely involved large-scale transfers of FRM, potentially driven by hectic historical afforestation campaigns and centralized seed supply systems (i.e., most FRM coming from a few nurseries). For instance, a single, large public Italian nursery (i.e., the Pieve Santo Stefano nursery, near the LVE natural population and the TRA-N area) has provided FRM for large reafforestation initiatives during the second half of the twentieth century, producing up to 2–2.5 million conifer seedlings annually during the peak years of national reforestation activities (Carabinieri, 2026).

The existence of plantations of mixed origin has not trivial consequences considering that several silver fir seed stands and Genetic Conservation Units in TEA and TRA macro-areas are plantations or in the reach of gene flow from plantations. For instance, within the TRA-N area, the plantations PON, POP, CMP, ERE, CMD, CRO, and BDP, which originated from a non-negligible proportion of FRM likely translocated over 600 kilometres southwards, are located inside seed stands (MASAF, 2026) and Genetic Conservation Units (EUFORGEN, 2026). The first obvious consequence of seed collection in stands of mixed origin is the unwanted lack of control on the genetic characteristics of the FRM being released by forest tree nurseries (Castro-Díez et al., 2026), and this calls for a thorough revision of both networks of silver fir seed stands and Genetic Conservation Units in the study area. Secondly, from a restoration genetics perspective, the conservation value of plantations also depends on whether geographically clustered adaptive patterns, possibly shaped by historical selective pressures, have been preserved or not (Thomas et al., 2014; Jia et al., 2020). In this regard, past southward translocations might be perceived as less promising to be now exploited as unintentionally done assisted migration experiments, although they could possibly provide relevant information about the relative outcome of south to north *vs*. north to south translocations (as in reciprocal transplant experiments). However, in the heterogenous landscapes of Southern Europe, the gene-environment associations could have been shaped by local conditions at a very fine spatial scale (e.g., Budde et al., 2023; Modica et al., 2024) and latitudinal translocations should be addressed taking into particular consideration local adaptation. Genome-wide assessment of future (mal)adaptation in natural populations, focusing on those that were sources of FRM, are needed to conclude about the possible adaptive value of southward translocations.

In terms of origin of FRM, the Abruzzo Apennines (ABA) displayed a contrasting pattern between plantations located on the northern and southern slopes of the Majella massif, which is a long-lasting biogeographical barrier for the species (Piotti et al., 2017). The ABA-N plantations, geographically in between CAPP and SAPP, were highly admixed. The lack of a regional reference cluster and their admixed origin, reflecting historical translocations from adjacent regions, challenge any provenance-based management of silver fir forest genetic resources in this area. In contrast, ABA-S plantations aligned closely with the regional reference cluster SAPP, which is consistent with localized seed sourcing as the uppermost SAPP natural populations are only a few kilometers distant (Santini et al., 2018). These findings, consistent with what was previously reported by Santini et al. (2018) based on a limited version of the reference dataset and on a more lenient assignment strategy, are particularly relevant. Conserving SAPP genetic resources, whether in natural populations or plantations, could be disproportionally important both for their high and unique genetic diversity (Piotti et al., 2017; Vajana et al., 2024; Balao et al., 2026) and because rear-edge populations could represent a valuable asset in supporting potential assisted migration strategies in Europe (Hampe and Petit, 2005; Chakraborty et al., 2024).

Another potential application of our results raises from the consideration that plantations with a strong genetic similarity with natural populations, such as those from TEA-S and ABA-S, may serve as effective seed sources or complement existing seed stands in areas where natural populations are particularly small and highly fragmented (Rovelli, 1995; Santini et al., 2018; Avanzi et al., 2024). Conversely, highly admixed plantations dominated by non-local material require cautious integration into restoration programs to avoid disrupting locally adapted gene

complexes and regional phylogeographic structure. While admixture can enhance standing genetic variation and provide potential adaptive flexibility under climate change, it also carries risks of maladaptation or outbreeding depression in specific environmental contexts (Edmands, 2007).

Finally, although our results indicated that silver fir plantations are storing substantial genetic diversity, yet natural populations remained the primary repositories of unique allelic variants. This was not a foregone outcome of our study, as most silver fir remnant populations in the Northern and Central Apennines have likely gone through a rapid shrinkage in the last centuries (Avanzi et al., 2024). The lower representation of private alleles in plantations suggested that, although afforestation had preserved a broad fraction of regional diversity, it had not fully captured the rare genetic variants present in remnant natural stands. Conversely, some alleles detected in plantations were absent from natural populations, reflecting the complex legacy of historical seed sourcing or introductions from unsampled or distant populations (Myking et al., 2016; Ivetić and Devetaković, 2017). The presence of private diversity on both sides highlights the irreplaceable role of natural populations as long-term reservoirs of evolutionary potential as well as how plantations could serve as complementary sources of genetic and phenotypic variation (Breed et al., 2013; Olsson et al., 2025). However, switching from a shallow genetic characterization of neutral genetic diversity to a deep, genome-wide assessment of genomic features potentially shaped by adaptive pressures, as well as homogenizing the sampling effort in natural populations and plantations to optimize the reciprocal characterization of private genetic diversity, will be key to properly understanding the peculiar conservation value of stands of natural and artificial origin.

### 4.2. Further insights from long-managed silver fir forests

The genetic characterization of the ARL plantation (known as Abetina Reale, in the TEA-S area) provided key insights into the origin, structure, and management history of this large, historically cultivated silver fir stand in the northern Apennines. A substantial proportion of individuals showed local genetic ancestry, supporting what was described in a report from the early 1900s that mentioned the practice of locally translocating naturally established seedlings to promote regeneration (Gori Montanelli, 1939). From a conservation perspective, this finding is particularly relevant because ARL now represents by far the largest silver fir stand of mostly local origin in the Northern Apennines, thus representing a preferred target for conservation plans. At the same time, a considerable percentage of individuals was assigned to the WALP genetic cluster. Spatial analyses of tree size help clarify the temporal dynamics that might have led to such genetic structure. Significant spatial autocorrelation in DBH indicates that trees of similar size are spatially aggregated, likely reflecting past management practices such as cohort-based planting (Pommerening and Stoyan, 2006). In particular, the predominance of individuals belonging to the regional reference cluster NAPP in the largest DBH classes suggests earlier establishment, differential growth under local environmental conditions, or a combination of both. Conversely, the predominance of WALP individuals in the smallest diameter classes, along with their spatial aggregation, likely indicates a more recent establishment and the abandonment of the practice described by Gori Montanelli (1939) in the last decades before ceasing management in the area in the 1960s.

In TRA-N, an area where silver fir has a millennium-long management history and was largely reforested at the beginning of the 19th century with a documented translocation of Boemian FRM (Gabbrielli, 1978; Motta et al., 2023), most individuals are of local origin. Although a non-negligible percentage of genotypes of Bohemian origin was detected (28.8%), which are quite evenly distributed across space and DBH classes, this might not rise major concerns in terms of outbreeding depression as Bohemian and local silver fir populations are fairly genetically similar, possibly due to a common post-glacial origin (e.g., Liepelt et al., 2009; Piotti et al., 2017). In a context where only the La Verna (LVE) and Bocca Trabaria (BTR) natural populations had previously been confirmed as of local origin (Piotti et al., 2017; Ducci et al., 2021), these findings indicated that the distribution of locally originated silver fir is more extensive than expected, thereby enhancing the prospects for the gradual re-naturalization of mixed beech-silver fir forests that likely characterized the Tuscan-Romagnol Apennines before extensive forest management.

The use of DBH as a proxy for tree age may limit the temporal precision of our reconstruction of plantation dynamics in TEA-S and TRA-N. Nevertheless, this readily measurable trait enabled us to analyse more than 900 individuals (460 in ARL and 459 in all TRA-N stands), a sample size that would not have been feasible had the age of each tree been estimated directly. We nonetheless consider the results reliable for three main reasons: 1) they are consistent with the limited historical information available, 2) the spatial clustering of similar DBH values confirmed that trees were planted simultaneously following clear-cutting across relatively large areas (DBH and year of plantation were indeed correlated in TRA-N plantations for which this information is available), and 3) the DBH-based reconstruction is consistent with the same temporal analysis on the year of plantation conducted in TRA-N (results not shown).

### 4.3. Limitations of the reconstruction and avenues opened by assessing the origin of plantations

The reconstruction of the origin of silver fir plantations in peninsular Italy was attempted in an area where natural populations are particularly admixed (i.e., Northern Apennines) and, more generally, the spatial genetic structure is rather complex (Piotti et al., 2017). This makes the assignment of planted individuals to their source genetic cluster inherently challenging. We therefore decided: i) to carefully characterize the natural populations from which FRM could have been collected, ii) to work at the genetic cluster level instead of at the population level to avoid problems related to admixture and clinal differences at short spatial scale, and iii) to select a rather strict assignment threshold (80%). Despite using a molecular marker set that provides improvable resolution power in reconstructing the origin of FRM, we were able to assign 73% of individuals sampled in plantations with high confidence. While genome-wide SNP data, increasingly available for large-scale studies in forest tree species (Pinosio et al., 2026; Guilbaud et al., 2026), would likely increase assignment precision, some uncertainty is expected to persist in areas characterized by extensive admixture or weak genetic structure (Olsson et al., 2026). Consistent with this expectation, the proportion of unassigned individuals was minimal in ABA-S, where most FRM originated from the genetically peculiar SAPP cluster.

Besides the historical value of reconstructing past translocations of FRM (Wagner et al., 2015; Jansen and Geburek, 2016), it is emerging that such an endeavor could shift our view to plantations as natural laboratories for assessing the performance of different tree provenances. Plantations of known origin may serve as unintentional experiments of assisted migration (see, for instance, Oggioni et al., 2024) or to validate predictions of future maladaptation based on genotype-environment associations and genomic offset (Francisco et al., 2025). This could prove particularly useful in geographic areas where provenance trials are scarce or absent (Fady and Rihm, 2022), such as Italy (Robson et al., 2018). In addition, while the evolutionary legacy of plantations remains poorly understood, accumulating evidence highlights their potential for immediate application in conservation (Breed et al., 2013; Santini et al., 2018; Jordan et al., 2019; Jia et al., 2020; Prakash et al., 2024). Whereas several potentially critical aspects still need to be investigated (e.g., the extent of maladaptive gene flow, the risk of outbreeding depression; see Laikre et al., 2010; Steinitz et al., 2011; Unger et al., 2016), plantations of local origin could serve as valuable starting points for management and conservation initiatives aimed at restoring, after centuries of

progressive anthropogenic simplification of forest composition (Avanzi et al., 2024), the structural complexity of Apennine beech forests. This may contribute to increasing their productivity, enhancing the resistance and resilience to both biotic and abiotic stressors, and delivering a wider range of ecosystem services (Jactel and Brockerhoff, 2007; Gamfeldt et al., 2013; Seidl et al., 2016; Versace et al., 2023). Regardless of their objective, initiatives based on the genetic diversity of plantations should be closely monitored, so that what is often perceived (at least in Italy) as unpredictable entities with an uncertain future could be turn into valuable forest genetic resources.

## CRediT authorship contribution statement

**Maria Beatrice Castellani:** Writing – review & editing, Writing – original draft, Formal analysis, Data curation, Conceptualization. **Andrea Piotti:** Writing – review & editing, Writing – original draft, Funding acquisition, Conceptualization. **Carlo Urbinati:** Writing – review & editing, Funding acquisition. **Giovanni Giuseppe Vendramin:** Writing – review & editing, Funding acquisition. **Camilla Avanzi:** Writing – review & editing, Writing – original draft, Resources, Funding acquisition, Formal analysis, Data curation, 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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## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2026.124391.

## Data Availability

Data will be made available on request.

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