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Phylogeography and climate shape the quantitative genetic landscape and range-wide plasticity of a prevalent conifer

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Abstract

The contribution of genetic adaptation and plasticity to intraspecific phenotypic variability remains insufficiently studied in long-lived plants, as well as the relevance of neutral versus adaptive processes determining such divergence. We examined the importance of phylogeographic structure and climate in modulating genetic and plastic changes and their interdependence in fitness-related traits of a widespread Mediterranean conifer (*Pinus pinaster*). Four marker-based, previously defined neutral classifications along with two ad hoc climate-based categorizations of 123 range-wide populations were analyzed for their capacity to summarize genetic and plastic effects of height growth and survival (age 20) in 15 common gardens. The plasticity of tree height and differential survival were interpreted through mixed modeling accounting for heteroscedasticity in the genotype-by-environment dataset. The analysis revealed a slight superiority of phylogeographic classifications over climate categorizations on the explanation of genetic and plastic effects, which suggests that neutral processes can be at least as important as isolation by climate as a driving factor of evolutionary divergence in a prevalent pine. The best phylogeographic classification involved eight geographically discrete genetic groups, which explained 92% (height) and 52% (survival) of phenotypic variability, including between-group mean differentiation and differential expression across trials. For height growth, there was high predictability of plastic group responses described by different reaction norm slopes, which were unrelated to between-group mean differentiation. The latter differences (amounting to ca. 40% among groups) dominated intraspecific performance across trials. Local adaptation was evident for genetic groups tested in their native environments in terms of tree height and, especially, survival. This finding was supported by $Q_{ST} > F_{ST}$ estimates. Additionally, our range-wide evaluation did not support a general adaptive syndrome by which less reactive groups to ameliorated conditions would be associated with high survival and low growth. In fact, a lack of relationship between mean group differentiation,

indicative of genetic adaptation, and predictable group plasticity for height growth suggests different evolutionary trajectories of these mechanisms of phenotypic divergence. Altogether, the existence of predictable adaptive-trait phenotypic variation for the species, involving both genetic differentiation and plastic effects, should facilitate integrating genomics and environment into decision-making tools to assist forests in coping with climate change.

KEYWORDS
adaptive traits, climate-driven selection, common garden, genotype-by-environment interaction, neutral variation, phenotypic plasticity

INTRODUCTION

The contribution of genetic adaptation and phenotypic plasticity modulating trait expression determines how forest trees thrive in complex environments. In evolutionary genetics, these two mechanisms have been traditionally considered to shape plants' phenotypes (Nicotra et al., 2010). In the simplest situation of comparable plasticity among individuals, intraspecific differences in adaptive traits assessed in a given environment can predict patterns of differentiation in other, untested environments. More often than not, however, the presence of genotype-by-environment (G × E) interactions points to differential plasticity at the intraspecific level (Matesanz & Ramírez-Valiente, 2019). In the last decades, a growing body of literature has scrutinized the role and adaptive implications of intraspecific differentiation in the plasticity of functional traits across functional types and biomes (Lortie & Hierro, 2022). However, the relative importance of plasticity and genetic differentiation contributing to phenotypic variability remains insufficiently studied (Leites & Benito-Garzón, 2023; Merilä & Hendry, 2014). Common garden experiments are instrumental to quantify such effects in long-lived plants and, hence, to evaluate the adaptive and acclimation potential of a species to face global change.

An important but often sidelined aspect of studying ecological and micro-evolutionary responses of plant species to environmental instability lies in the interpretation of neutral versus adaptive processes determining intraspecific differentiation and plasticity (Ovaskainen et al., 2011). Neutral variation is determined, among others, by past recolonization routes following glaciations, genetic bottlenecks and isolation by distance. Associated with genetic drift and migration, such demographic processes leave a phylogeographical mark that typically leads to a hierarchical population structure not necessarily related to true adaptive differentiation. While this structure can be effectively summarized in several genetic groups (or "gene pools"), in some instances, however, the intraspecific neutral structure is so complex that defining such pools may turn into a fairly subjective practice (de Villemereuil et al., 2022). Alternatively, spatial heterogeneity in environmental conditions (climate, soil, fire, biotic pressures, etc.) can impose divergent selection pressures and lead to locally adapted geographic variants, or ecotypes (Kawecki & Ebert, 2004; Lortie & Hierro, 2022). Demonstration of local adaptation requires that differences in phenotypic traits between ecotypes are associated with environmental differences at origin (e.g., climate) beyond what could be expected to arise from neutral divergence (Eckert et al., 2010), while showing increased fitness under their "local" environment (Kawecki & Ebert, 2004).

In practical terms, unraveling the contribution of phylogeographical structure and adaptive processes to the explanation of genetic differentiation and plasticity of functional traits is cumbersome, because the spatial population structure resulting from evolutionary histories often parallels that of environmental variation (Desdevises et al., 2003; Sohail et al., 2019). One such example (Serra-Varela et al., 2015) is maritime pine (*Pinus pinaster* Ait.), a model pine species from the western Mediterranean basin harboring large phenotypic differentiation for life-history traits across its distribution range (Di Matteo & Voltas, 2016; Santos-del-Blanco et al., 2013; Zas et al., 2020), as well as large neutral variation characterized by strong spatial population structure (Bucci et al., 2007; Jaramillo-Correa et al., 2015). Both neutral and adaptive variations have been shown to be highly imbricated among each other for characteristics such as drought tolerance (Grivet et al., 2011) or secondary metabolites (López-Goldar et al., 2019).

For characterizing patterns of plant adaptation, comprehensive investigations of phenotypic variation for key functional traits are still lacking for most widespread forest species. Maritime pine is not an exception, despite previous efforts aimed at disentangling the importance of genetic and plastic effects on tree growth, which involved representative populations but incomplete testing

conditions (e.g., Alía et al., 1997; Correia et al., 2010; Di Matteo & Voltas, 2016). While these studies revealed both population differentiation and differential plasticity, they were not conclusive regarding the range-wide population structure of the species or the importance of neutral versus adaptive processes governing it. In this work, we evaluated intraspecific patterns of maritime pine growth and survival using mixed modeling of G × E interactions of a highly unbalanced multienvironment trial network (~25% population–trial combinations available). Mixed models are appropriate for interpreting variation in phenotypic plasticity (Arnold et al., 2019), while dealing with the existing lack of balance in the dataset. In particular, plasticity measures can be readily embedded in a mixed-model framework through variance–covariance estimation of random plastic effects (Denis et al., 1997). These metrics allow quantifying predictable plasticity (in terms of e.g., reaction norm slopes) and residual plasticity (potentially indicative of local adaptation) resulting from environmental variation acting at the genotypic level (e.g., individual, population, or group of populations underlying a hierarchical structure). Accurate inferences can also be drawn on mean genotypic responses underlain by shifts in allele frequencies. Altogether, mixed models can provide comprehensive evidence of overall differentiation among genetic entities along with variation in such differentiation across environments linked to differential plasticity. If present, the specificity of plastic responses may indicate that they are heritable and therefore a target for selection (Pigliucci et al., 2006). For example, a higher plasticity for fitness traits such as height growth is expected to confer broader tolerance to varying environmental conditions and, therefore, an increased ecological niche breadth (Reed et al., 2011). However, plasticity can also hinder adaptation by modifying the distribution of phenotypes in the population, shielding it from natural selection (Fox et al., 2018).

We employed different classifications of maritime pine populations based on either putatively neutral genetic markers (i.e., previously defined neutral groups) or climatic information at different spatial resolutions (i.e., climate-based groups). These classifications were analyzed, alone and in combination, for their capacity to explain genetic differentiation and plastic effects contributing to broad phenotypic changes for height growth. They were also used for interpreting intraspecific variability in survival as the ultimate component of plant performance and fitness and, therefore, as the main determinant of demographic rates which are subject to climate variation (Johnson et al., 2018). The adopted strategy exemplifies how leveraging the sparse information encompassed in range-wide transnational networks of common gardens may enable the delineation of broad patterns of phenotypic differentiation. We used hierarchical mixed models to better understand the role of adaptive differentiation (including potentially adaptive plasticity), in addition to neutral divergence, in shaping phenotypic diversity for fitness-related traits. We hypothesized that (1) for a species with a strong population structure such as *P. pinaster* (Bucci et al., 2007; Burban & Petit, 2003), intraspecific differentiation in fitness-related traits is jointly explained by phylogeography and historical climate at the origin of populations; and (2) as the joint result of its evolutionary history, fragmented distribution and adaptation to local conditions, the species' quantitative genetic diversity can be effectively summarized in a limited number of groups that incorporate a phylogeographical (neutral) structure but also integrate specific climatic properties. Plasticity patterns resulting from the arrangement that best summarized the existing quantitative variability were then analyzed and subsequently interpreted in terms of the significance and adaptive value of genetic differentiation and phenotypic plasticity for the species.

MATERIALS AND METHODS

Plant material

Seed sources from 123 populations of maritime pine representing most of the natural distribution range of the species (Appendix S1: Section S1; Table S1), which spans southwestern Europe and northern Africa, were used (Figure 1a; Appendix S1: Section S1). The populations originated from Spain (76 populations), Morocco (18), Corsica (12), mainland Italy (6), mainland France (5), Portugal (3), Algeria (1), Sardinia (1) and Tunisia (1) (Data [spreadsheet format] available in Zenodo at https://doi.org/10.5281/zenodo.8079551). Climatic variables at origin were obtained from two alternative databases for the period of 1961–1990, as surrogates of the conditions under which populations have evolved: CRU (Climatic Research Unit, CRU TS 3.24; Harris et al., 2014) and WorldClim (Global Climatic Data v. 1.4; Hijmans et al., 2005). CRU provided climate series on a coarse resolution (spatial resolution of 0.5° × 0.5° ≈ ca. 50 × 50 km for intermediate latitudes). Alternatively, WorldClim (hereafter, WCL) supplied high-resolution estimates of local climate with a spatial resolution of 1 km^2. On the one hand, the coarser CRU may account more faithfully for patterns of population differentiation in a wind-pollinated, widely distributed conifer such as *P. pinaster*, as found for the taxonomically close *P. halepensis* (Voltas et al., 2018). On the other hand, the finer WCL may incorporate better the influences of

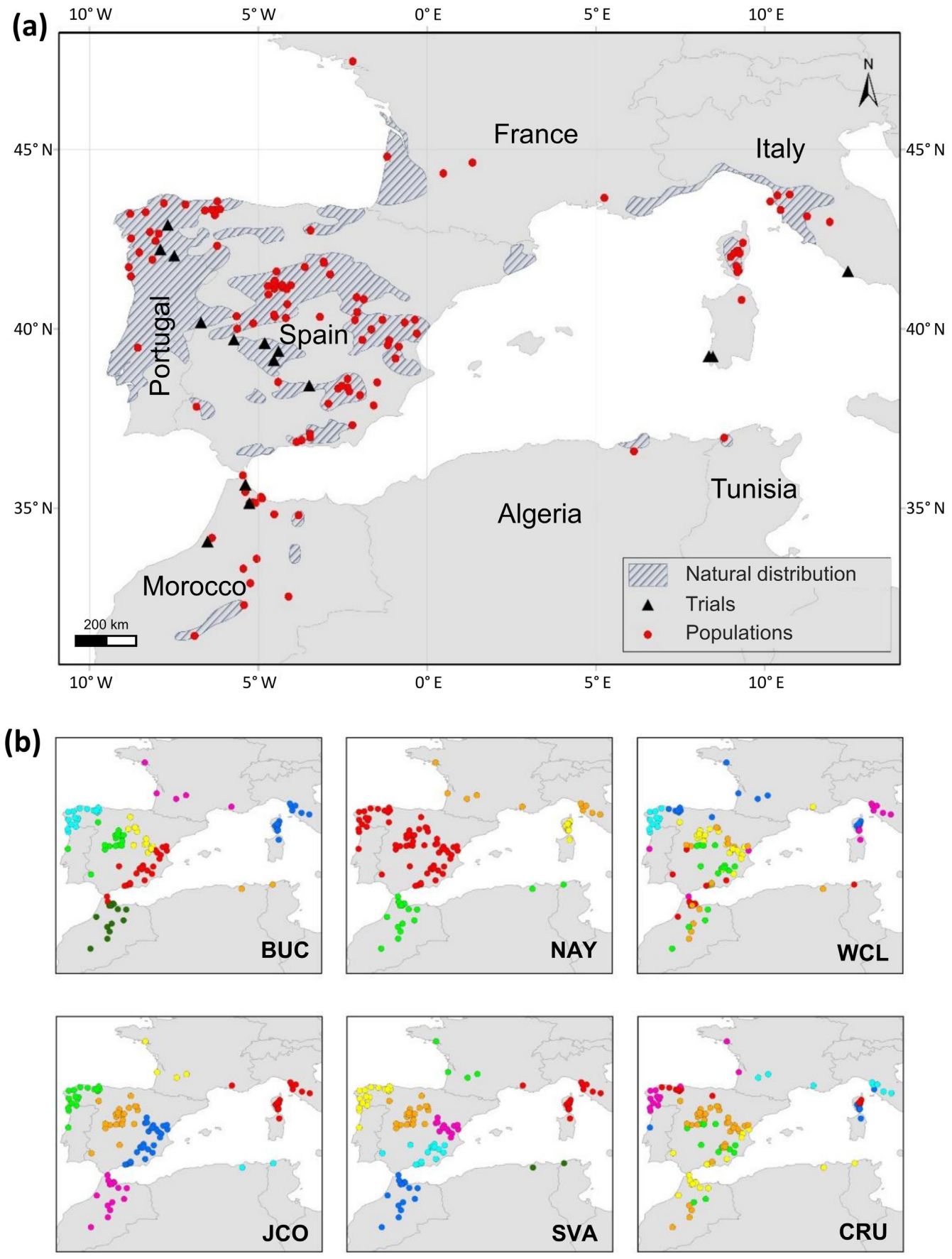

FIGURE 1 Legend on next page.

topography and aspects of local climate, which can play an important role in genetic adaptation. In both cases, the climatic variables were selected based on earlier identification of climate drivers of ecotypic variation in Mediterranean pines (Tapias et al., 2004), and included mean annual temperature (MAT), maximum temperature of the warmest month (i.e., July; TMX), minimum temperature of the coldest month (i.e., January; TMN), temperature annual range (i.e., TMX – TMN; TAR), mean annual precipitation (MAP) and mean summer precipitation (MSP).

Study sites and field measurements

Provenance trials (common gardens) were available at 15 locations distributed across the western Mediterranean basin (Italy, Morocco and Spain; Figure 1a). Trial MAT ranged from 11.8 to 18.4°C, and trial MAP from 481 to 1154 mm. The three Italian trials were established within the framework of the FAO/Silva Mediterranea international initiative (Chambel et al., 2013), while the remaining trials were sponsored by regional (three trials in Galicia, northwestern Spain) or national initiatives (six trials in Spain, three trials in Morocco). Phenotypic data from central Spain and Morocco were obtained from Vizcaíno-Palomar et al. (2019). Geographic and climatic details of trials are provided in Appendix S1: Section S1; Table S2. As a result of the different years of establishment, objectives and resources available to each experiment, not all populations were tested at every site. This led to an extremely unbalanced dataset, which is a typical situation in transnational multienvironment forest genetic trials (e.g., *Pinus* spp.; Chambel et al., 2013; Appendix S1: Section S1, Table S3).

Total height at age 20 years was used to characterize the potential of populations to perform across a range-wide environmental gradient (Appendix S1: Section S1, Table S4). For each population, a best linear unbiased estimate (BLUE) of mean tree height was obtained in each trial by fitting a linear mixed-effects model accounting for the experimental setup and intraplot (between-tree) variability. Additionally, data on tree survival were obtained from the nearest age to the target age of 20 years (Appendix S1: Section S1, Table S4). Percentages of living trees per population at the trial level were used for analysis. Prior to analysis, survival rates per population–trial combination (mostly ranging between 40% and 100%) were angular transformed. We did not use mixed-effects logistic regression to analyze survival responses across trials because of convergence issues when fitting mixed models (Appendix S1: Section S2).

Classification of populations into putatively neutral or climate-based groups

Several studies have investigated the genetic refuges of maritime pine during the last Pleistocene glaciations, describing a variable number of neutrally differentiated (or phylogeographic) lineages and their respective postglacial migration routes (Bucci et al., 2007; Burban & Petit, 2003). The definition of genetic groups accounting for most neutral variation of the species is, therefore, contentious, and contingent on the number of populations and type of genetic marker(s) used in each case. For this study, we categorized the available 123 populations according to four alternative phylogeographic classifications (Figure 1b):

1. Bucci et al. (2007) identified eight genetic groups based on five chloroplast microsatellites and 48 populations (hereafter, BUC).
2. Naydenov et al. (2014) identified four genetic groups based on eight nuclear microsatellites and 27 populations (hereafter, NAY).
3. Jaramillo-Correa et al. (2015) defined seven genetic groups based on nine nuclear microsatellites and 1745 supposedly neutral SNPs characterizing 36 populations (hereafter, JCO).
4. Serra-Varela et al. (2015) delineated eight genetic groups based on 266 hypothetically neutral SNPs in 45 populations (hereafter, SVA).

The allocation of populations to previously defined genetic groups was visually performed based on range

FIGURE 1 Distribution range of *Pinus pinaster* and assignment of populations to genetic or climate-based groups. (a) Distribution range of the species (hatched area; EUFORGEN, http://www.euforgen.org/species/pinus-pinaster/) and location of the 123 populations (red dots) included in the 15 trials (black triangles). (b) Assignment of populations to previously defined neutral groups following the classifications of Bucci et al. (2007) (BUC; eight groups), Naydenov et al. (2014) (NAY; four groups), Jaramillo-Correa et al. (2015) (JCO; seven groups) and Serra-Varela et al. (2015) (SVA; eight groups), along with alternative categorizations of populations into climate-based groups according to WCL (high resolution) and CRU (coarse resolution) climate records (seven groups in both cases). Each (arbitrary) dot color indicates a particular genetic group or a climate-based group, the latter as identified in the constellation plot of Appendix S1: Section S4; Figure S2 (for WCL) and Appendix S1: Section S4; Figure S3 (for CRU) after cluster analyses.

maps available for each of the four classifications. The procedure followed consisted of graphically overlapping the maps provided in the original papers with the location map of populations as shown in Figure 1a, which resulted in the groups outlined in Figure 1b. We consider this assignment to be accurate enough, as there were very few uncertain cases. For the sake of comparison, the original populations used as the basis for each genetic grouping (BUC, NAY, JCO or SVA) were imposed on the maps corresponding to each classification (Appendix S1: Section S1; Figure S1). In any case, we assumed that the final assignment may be slightly biased because some populations are prone to show large-scale genetic admixture (as described in e.g., Serra-Varela et al., 2015).

Additionally, hierarchical cluster analysis (Ward's method) was used to identify ecotypes with potentially divergent adaptive characteristics triggered by climate, or climate-based groups (Tapias et al., 2004). To this end, each population was assigned to a different group based on climatic information at the origin using either coarse resolution (CRU) or high resolution (WCL) data. The climate variables used were MAT, MAP, TAR, MSP, TMX and TMN. Both the set of trials and the set of populations used in this study were representative of the climatic conditions where maritime pine is found naturally (Figure 2a,b).

Data analysis

Linear mixed-effects models

As a starting point, tree height or survival data were subjected to hierarchical mixed-effects analysis of variance (ANOVA) with fixed genetic or climate-based groups and random trial and group-by-trial interaction as follows (random effects appear underlined):

$$Y_{ijk} = \mu + G_i + \underline{T_k} + \underline{(GT)_{ik}} + \underline{e_{ijk}}, \quad (1)$$

where Y_{ijk} is the estimate of the jth population of the ith group in the kth trial, μ is the general mean, G_i is the fixed effect of the ith group, $\underline{T_k}$ is the random effect of the kth trial, $\underline{(GT)_{ik}}$ is the random effect of interaction between the ith group and the kth trial, and $\underline{e_{ijk}}$ is the random residual effect of the jth population nested to the ith group at the kth trial. Note that the population nested to group effect was subsumed in the random residual term to facilitate the comparison of models regarding their different grouping structures (described in the next paragraph). Plastic effects therefore included trial (denoting general, or species level, plasticity) and group-by-trial variability (representing differential, or group-level, plasticity), and were considered as random variation (i.e., drawn from the entire set of trials). Here, the group-specific G_i effects were considered fixed because the phylogeographic and climate-based classifications had a relatively low number of groups ($\leq$8) and our primary focus was to summarize broad geographic patterns of quantitative variation for the species.

Each classification strategy (phylogeographic or climate-based) was characterized by means of marginal and conditional R^2 values (Nakagawa & Schielzeth, 2013), which inform on the variance explained by the fixed factor alone (marginal R^2_m) or together with the random factors of the model (conditional R^2_c). In our case, R^2_m quantified the (fixed) contribution of mean differences among genetic or climate-based groups to the explanation of tree height or survival records. In turn, R^2_c expressed the joint importance of group-level and plastic changes (i.e., due to fixed and random effects, respectively, the latter including both general and group-specific plasticity). As an extension of Equation (1), a model that jointly included the best genetic and climate-based classifications, along with their interactions with the random trial effect, was also fitted to the data.

To further explore the relative contribution of each source of variation, Equation (1) was simplified by (1) excluding the random interaction term $\underline{(GT)_{ik}}$, hence ignoring differential plasticity among groups, and (2) excluding both the fixed G_i effect and the $\underline{(GT)_{ik}}$ term, hence ignoring mean differences among groups and also their differential plasticity. Finally, we divided the total set of populations into two subsets by using the best phylogeographic and climate-based classifications: the first subset was composed of populations assigned to the most common climate-based group identified within each genetic group (or subset of consistent populations); a second subset comprised those populations assigned to other climate-based groups identified within each genetic group (conflicting populations). Equation (1) was then fitted to each subset separately using either the neutral or the climate-based classification as a grouping criterion. In this way, we addressed the issue of partial confounding between putatively neutral and climate-driven adaptive effects for tree height and survival because confounding is maximized in the "conflicting" subset and minimized in the "consisting" one. The adequacy of different classifications and their simplified alternatives was assessed using Akaike's information criterion (AIC) based on the full maximum likelihood (ML) method to compare different fixed effects structures in the model. AIC was interpreted in the smaller-is-better form.

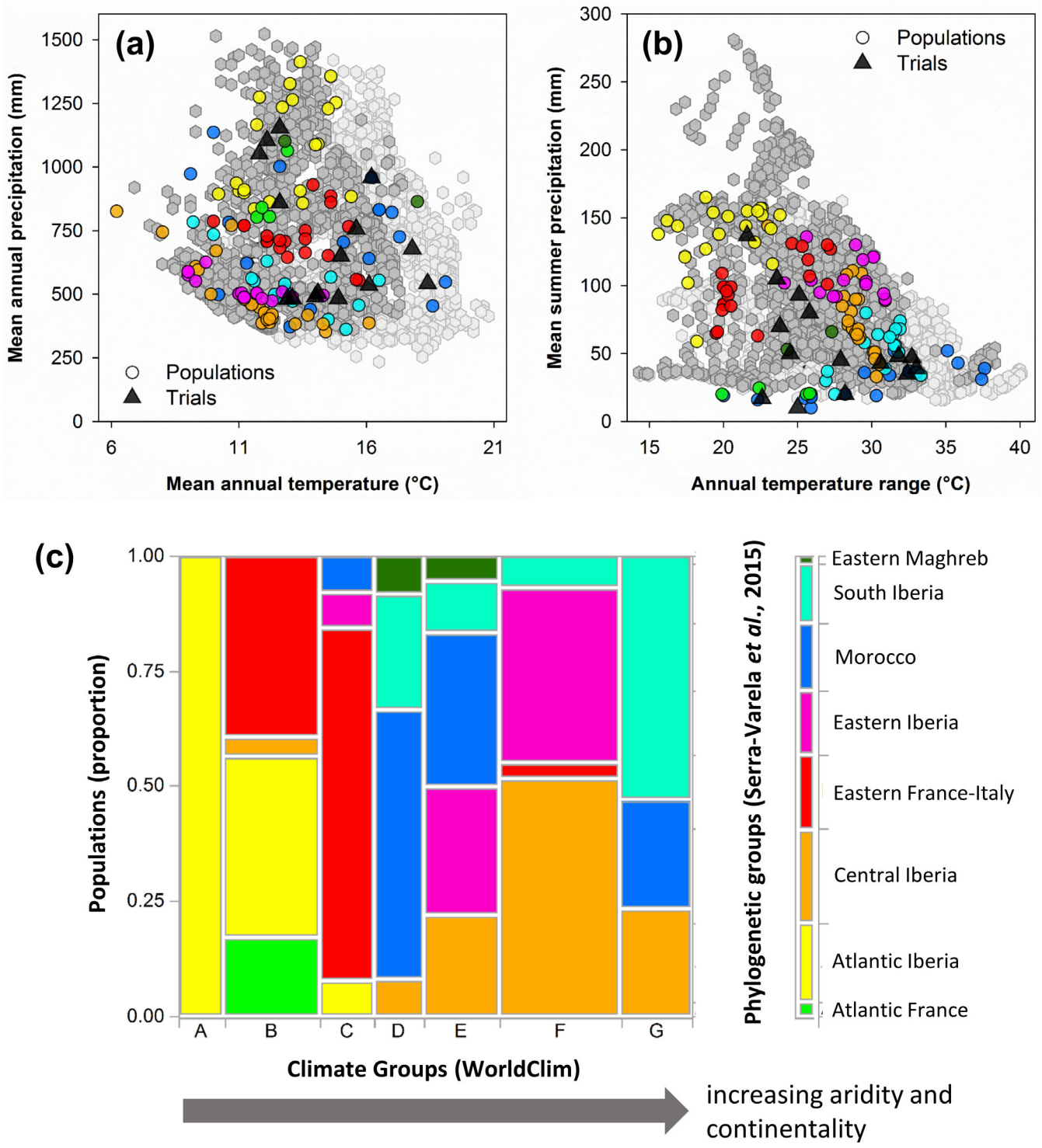

FIGURE 2 Autoecology of *Pinus pinaster* and correspondence between genetic and climate-based groups. (a, b) Autoecology diagrams based on WorldClim (WCL) data (resolution = 10′, the species distribution is based on EUFORGEN; see caption of Figure 1) with trials depicted as black triangles and populations depicted as colored circles. The dark gray dots represent historical climate conditions (1961–1990) while the light gray dots represent future climate conditions (i.e., the period 2071–2100) under a "moderate" scenario (representative concentration pathway RCP 4.5 W m^2). (c) Mosaic plot summarizing the correspondence between the classification of populations based on the genetic groups of Serra-Varela et al. (2015) and the categorization of populations into climate-based groups according to WCL. The area of each tile in the mosaic plot is proportional to the number of populations of a given genetic group assigned to a particular climate-based group. The dot (or tile) color denotes a particular genetic group as shown in Figure 1b.

Mixed-effects models for the analysis of phenotypic plasticity

After selecting a grouping scheme of populations that best summarized genetic and plastic effects on tree height and survival for the species, we evaluated a number of mixed models accounting for interaction and heteroscedasticity in genotype-by-environment tables. For model evaluation, the range of height error variances across trials (0.19–1.83 m^2) suggested that population–trial means were estimated with sufficiently similar precision (alternatively, we tested a weighting scheme based on reciprocals of trial error variances with similar results; Appendix S1: Section S2).

These models provided quantitative measures useful for explaining G × E interactions and, therefore, differential phenotypic plasticity that can be embedded in a mixed-modeling framework (Arnold et al., 2019; Denis et al., 1997; Morrissey & Liefting, 2016). They are extensions of Equation (1) assuming different variance–covariance structures for the group-by-trial interaction term. In particular, the allocation of populations to groups and the use of random effects for the group-by-trial classification allow for the borrowing of information across groups when estimating mean height or survival at the group level. This increases precision, particularly for groups with a low number of populations. Two different sets of models were fitted: (1) assuming uniform deviations of populations from group means across trials (i.e., homogeneous $\underline{e_{ijk}}$ in Equation 1) or (2) allowing for trial-specific deviations of populations from group means (i.e., heterogeneous $\underline{e_{ijk}}$ in Equation 1). In this last case, the trials were assigned to three classes having high, medium and low residual variances for height or survival to facilitate convergence (Appendix S1: Section S1, Table S3).

We applied the framework initially proposed by Denis et al. (1997), which represents a unified method by which mixed models of multitrial data can be expressed and compared (Appendix S1: Section S2). This framework can accommodate more recent approaches for analyzing phenotypic plasticity such as random regression (Arnold et al., 2019). Each model is defined as the sum of three components: the fixed terms, the random terms, and the residual term. In some cases, one component may vanish from the model, but for interpretation purposes this distinction is adequate. Specifically, the main term of interest here is $(GT)_{ik}$ as defined in Equation (1), which represents group-by-trial effects. This term can be modeled in a very flexible manner, and several plasticity metrics for describing such effects were obtained using appropriate variance–covariance (VCOV) structures. The mixed models tested can be summarized as follows (outlined in Appendix S1: Section S2, Table S5):

1. Model 1: (Additive Mixed Model, ADMM). This is the simplest model in which the *I* groups do not differ in phenotypic plasticity.
2. Model 2: (General Heteroscedastic Mixed Model, GHMM). This model extends the additive model by attributing a different variance component to each group, as a metric quantifying the magnitude of plastic effects at the group level. It was first proposed by Shukla in its fixed variant (Shukla, 1972).
3. Model 3: (Linear Random Regression Mixed Model, RRMM). This model describes the variance in plasticity among groups in terms of random linear reaction norms in response to an environmental variable, as described by Arnold et al. (2019). However, this variable is not here defined as an explicit environmental driver; instead, it takes the form of the mean trial value, as first proposed by Finlay–Wilkinson (Finlay & Wilkinson, 1963). The group λs (Appendix S1: Section S2, Table S5) can be interpreted in terms of the reaction norm slope, that is predictable plasticity (Gomulkiewicz & Kirkpatrick, 1992).
4. Model 4: (Heterogeneous Linear Random Regression Mixed Model, HRMM). This model extends the linear random regression model (model 3) to allow for heterogeneity in residual interaction variance among groups (i.e., heterogeneous random deviations from reaction norm slopes, or unpredictable plasticity; Denis et al., 1997).
5. Model 5: (Factor Analytic Multiplicative Mixed Model, FAMM). This is the mixed model version of the additive main effects and multiplicative interaction model with one multiplicative component (Kempton, 1984). The group λs (Appendix S1: Section S2; Table S5) can be interpreted in terms of the reaction norm slope to the value of a hypothetical environmental variable for each trial not necessarily driving the trial main effect. This hypothetical, or latent, variable often summarizes most patterns present in G × E interactions (Malosetti et al., 2013).

A schematic summary of the models evaluated can be found in Figure 3. Their adequacy was compared by computing AIC based on the restricted maximum likelihood (REML) method. AIC involves a penalty for the number of parameters in the VCOV structure, which favors parsimonious models. Multiple mean comparisons among groups across trials for the best fitting models (for height or survival) were performed using Fisher's least significant difference test (LSD) taking into account that, for unbalanced data, the standard error of a difference is not constant for all comparisons. Previously, Wald-type *F*-statistics were used to make inferences about the fixed effect of groups. The analyses were performed using the MIXED procedure of SAS/STAT (Littell et al., 1996).

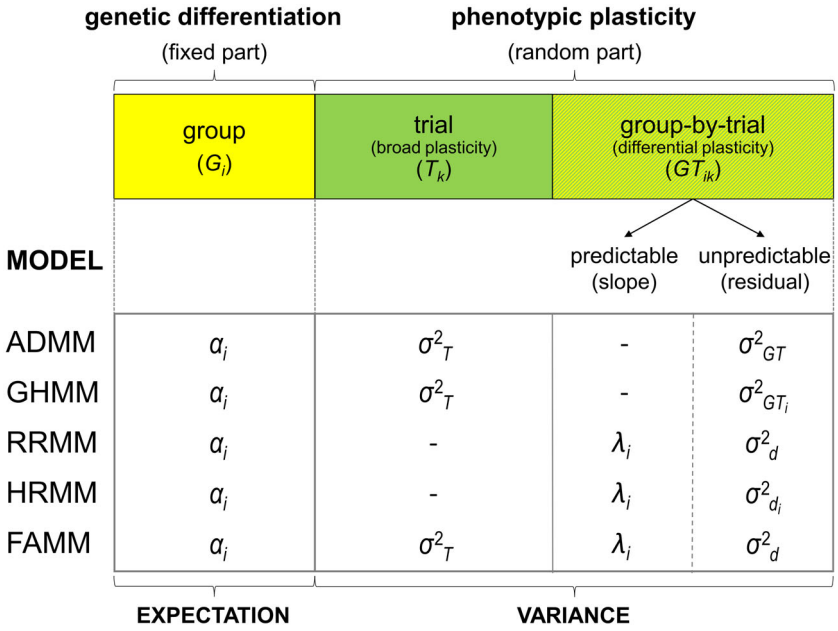

FIGURE 3 Schematic summary of mixed models applied for the estimation of the mean value (α) of *I* fixed groups of populations and their phenotypic plasticity evaluated in *K* random trials. These models account for interaction and heteroscedasticity in genotype-by-environment tables and are defined as follows: ADMM, additive mixed mode; FAMM, factor analytic multiplicative mixed model; GHMM, general heteroscedastic mixed model; HRMM, heterogeneous linear random regression mixed model; RRMM, linear random regression mixed model. Extended details are provided in Appendix S1: Section S2.

Probability of outperformance and consistency of performance

An assessment of phenotypic plasticity, as described above, characterizes differential plasticity among groups but it is desirable to complement this measure with the estimated mean group value across trials to quantify the relative superiority of each group (Piepho, 1998). Accordingly, the concept of phenotypic plasticity in tree height can be reassessed by the joint examination of group-level means and their variability across environments. In this framework, we evaluated the risk of poor performance over the entire distribution range of the species (as represented by 15 trials) in terms of the probability of one group outperforming another group (Eskridge & Mumm, 1992; revised in Dias et al., 2022). This probability can be computed as:

$$\Pr(D_j > 0) = \Phi\lfloor \partial/\sigma_D \rfloor, \quad (2)$$

where D_j is the difference of performance between group 1 and group 2 in trial j, Φ is the cumulative distribution function of the standard normal curve, $\delta = \mu_1 - \mu_2$, and σ_D is the standard deviation of a difference D_j in a randomly chosen environment. For the preferred model (HRMM, see Results), its associated variance σ^2_D equals (Piepho, 1998):

$$\sigma^2_D = (\lambda_1 - \lambda_2)^2\sigma^2_w + \sigma^2_{d_1} + \sigma^2_{d_2}, \quad (3)$$

where $\sigma^2_w = 1$ and $\sigma^2_{d_i}$ is a residual heterogeneous stability as defined in Appendix S1: Section S1; Table S5.

Also, different joint effects of varying trial characteristics, soil and climate conditions potentially eliciting local adaptation in terms of tree height and survival of groups were evaluated through a consistency of performance analysis (Flores et al., 1998; Ketata et al., 1989) across large ecoregions. This procedure is based on the simultaneous use of the average height rank of populations across trials (μ_{RANK}) and its standard deviation (σ_{RANK}) for each group, and allowed for the relative classification of groups into four different classes: (1) consistently superior (high μ_{RANK} and low σ_{RANK}); (2) inconsistently superior (high μ_{RANK} and high σ_{RANK}); (3) consistently inferior (low μ_{RANK} and low σ_{RANK}); and (4) inconsistently inferior (low μ_{RANK} and high σ_{RANK}). This was independently done by assigning each of the available 15 trials to four environmentally homogeneous subareas, or ecoregions, according to the division by Olson et al. (2001), as follows: Atlantic Spain (represented by four trials), central Spain (five trials), Italy (three trials), and Morocco (three trials). The assignment of trials to ecoregions (shown in Appendix S1: Section S1, Figure S1) was intended to test for local adaptation for the following four genetic groups: Atlantic Iberia (for Atlantic Spain trials), Central Iberia (for central Spain trials), Eastern France–Italy (for Italian trials) and Morocco (for

Moroccan trials). In this way, we sought to clarify whether the overall conclusions of the range-wide analysis held true across broad Mediterranean regions or, alternatively, the data on tree height and survival could provide clues on the existence of locally adapted gene pools of the species.

Quantitative genetic differentiation (Q_{ST})

To estimate the amount of quantitative population genetic differentiation for tree height, the Q_{ST} parameter was obtained as the ratio between the amount of genetic variance among populations (σ_P^2) and the total genetic variance of the trait ($\sigma_P^2 + 2\sigma_w^2$ in diploid organisms, with σ_w^2 as genetic within-population variance) following González-Martínez et al. (2002) and Whitlock (2008). For comparison purposes with the population neutral differentiation through the F_{ST} parameter (see below), Q_{ST} was computed (1) for each trial independently, including the entire set of populations in the analyses (i.e., at the species level), or (2) across trials, for each (SVA-based) genetic group separately. In the first case, the relevance of plastic responses to varying environmental cues due to population-by-environment effects, which could bias Q_{ST} estimation, was obviated. In the second case, Q_{ST} estimates at the group level obtained across trials were little affected by population-by-environment effects because most genotype-by-environment interactions could be attributed to differential plasticity among genetic groups (see *Results* section).

For estimating Q_{ST} values, and given that the available trials were not designed to provide heritability values, we evaluated the relevance of varying narrow-sense heritability (0.1, 0.2, and 0.5), being 0.2 a reasonable estimate for tree height based on published evidence (e.g., Zas et al., 2004). Standard errors and confidence intervals of Q_{ST} were obtained by parametric bootstrap resampling (1000 simulations). Q_{ST} estimates were compared with the population neutral differentiation F_{ST} parameter also reported within and across groups in Rodríguez-Quilón et al. (2016). A good matching between the genetic groups (SVA-based) and those reported in Rodríguez-Quilón et al. (2016) allowed for such comparison. Detailed information can be found in Appendix S1: Section S3.

RESULTS

Allocation of populations to putatively neutral or climate-based groups

The allocation of populations to genetic groups based on four previously defined neutral classifications is shown in Figure 1b. Overall, there was a fairly good representation of populations per group regardless of classification, with at least four populations present at the group level. The exception was the Eastern Maghreb (Algeria–Tunisia) group identified in three classifications, for which only two populations were available. Alternatively, the cluster analysis produced seven climate-based groups using either WCL (Appendix S1: Section S4, Figure S2) or CRU (Appendix S1: Section S4, Figure S3). The WCL-based and the CRU-based groupings captured 77% and 83% of variability among populations in climate records, respectively. All seven climate-based groups had a relatively large number of populations (≥5), regardless of climate database (Figure 1b).

Mixed models testing for alternative classifications of populations

The mixed-effects model for tree height accounting solely for general plasticity, that is, disregarding between-group mean differences and differential plasticity, had a R_c^2 of 0.80 (Table 1). This indicated that most height variability was the result of broad plasticity at the species level. Indeed, there were almost three-fold differences in height at age 20 among extreme trials (from 5.50 ± 0.52 m in Espinoso (central Spain) to 13.53 ± 0.33 m (±standard deviation [SD]) in A Merca [NW Spain]) (Appendix S1: Section S1; Table S2). When accounting for both between-group differences and differential plasticity among genetic groups (the full model in Table 1), the classification that gave the best fit was SVA, which showed the highest R_c^2 (0.92) and lowest AIC (1225.3) (Table 1). SVA also exhibited the highest R_m^2 (0.13, accounting solely for between-group differences) and significant group-by-trial effects (i.e., differential plasticity among groups), as indicated by its lower AIC compared with a simplified model excluding $\underline{(GT)_{ik}}$ (1261.6) (Table 1). In comparison, the two climate-based classifications performed worse than the phylogeographic classifications (i.e., with higher AIC), with no relevant differences between them (i.e., similar R_c^2 and AIC values; Table 1).

We also found large variability in survival (Table 1), although broad differences among trials were lower than those of tree height (R_c^2 for a simplified model accounting solely for environmental effects = 0.40). Mean survival across trials varied between $48.4 \pm 20.2\%$ in Ain Rami (Morocco) and $90.3 \pm 5.5\%$ in Domusnovas (Sardinia) (Appendix S1: Section S1, Table S2). The classifications that better explained both mean differences between groups and their differential survival among trials were BUC (R_c^2 of 0.56 and AIC of −311.5) and SVA (R_c^2 of 0.52

TABLE 1 Goodness-of-fit statistics of linear mixed-effects models for the explanation of mean differences between groups (fixed group, *G*) and plastic effects (random trial and group-by-trial interaction, $T + GT$) of tree height and survival.

Trait	Common plasticity (*T* only)	Phylogeographic classification[a]				Climate-based classification[a]		Joint model
		BUC	NAY	JCO	SVA	WCL (high res.)	CRU (coarse res.)	
Height								
Full model assuming mean differences and differential plasticity between groups ($G + T + GT$)								
R^2_m (marginal)	...	0.10	0.07	0.09	0.13	0.05	0.07	0.14
R^2_c (conditional)	...	0.89	0.86	0.89	0.92	0.87	0.86	0.93
AIC	...	1299.6	1346.7	1313.6	1225.3	1386.4	1384.6	1214.1
Restricted model assuming common plastic responses between groups ($G + T$)								
R^2_m	...	0.10	0.07	0.09	0.13	0.05	0.07	0.15
R^2_c	...	0.86	0.85	0.85	0.88	0.83	0.84	0.89
AIC	...	1311.1	1347.0	1347.9	1261.6	1406.8	1389.5	1246.1
Restricted model assuming only general plasticity (lack of mean group differences and of differential plasticity) (T)								
R^2_m	0							
R^2_c	0.80							
AIC	1463.2							
Survival								
Full model assuming mean differences and differential plasticity between groups ($G + T + GT$)								
R^2_m	...	0.13	0.06	0.10	0.12	0.06	0.04	0.18
R^2_c	...	0.56	0.37	0.52	0.52	0.55	0.49	0.63
AIC	...	−311.5	−244.2	−302.8	−297.2	−283.3	−265.0	−333.8
Restricted model assuming common plastic responses between groups ($G + T$)								
R^2_m	...	0.15	0.06	0.11	0.14	0.05	0.05	0.18
R^2_c	...	0.45	0.36	0.42	0.43	0.38	0.38	0.48
AIC	...	−302.1	−246.4	−289.6	−292.4	−254.1	−255.7	−316.8
Restricted model assuming only general plasticity (lack of mean group differences and of differential plasticity) (T)								
R^2_m	0							
R^2_c	0.40							
AIC	−237.6							

[a]BUC, Bucci et al. (2007); NAY, Naydenov et al. (2014); JCO, Jaramillo-Correa et al. (2015); SVA, Serra-Varela et al. (2015); WCL, WorldClim (Hijmans et al., 2005); CRU, Climatic Research Unit (Harris et al., 2014).

Note: Marginal and conditional R^2 values along with Akaike's information criterion (AIC) statistics are shown for the different models. The results of a full model including *G*, *T* and *GT* (see Equation 1 of main text) are presented for different classifications of populations (phylogeographic or climate-based). Likewise, two reduced models are tested: one assuming mean differences between groups but common plastic effects across groups (i.e., excluding *GT*), and another accounting exclusively for general plasticity (i.e., excluding both *G* and *GT*). The last column showcases the results of a joint model including the best combination (i.e., with smaller AIC) of a phylogeographic (SVA) and a climate-based (WCL) classification.

and AIC of −297.2) (Table 1). Indeed, BUC and SVA exhibited the highest R^2_m (0.13 and 0.12 respectively) and significant group-by-trial effects (i.e., differential survival of groups), as indicated by lower AIC compared with simpler alternatives excluding $\underline{(GT)_{ik}}$ (Table 1). In this case, the climate-based classifications and, especially, the WCL-based grouping showed similar goodness-of-fit ($R^2_c = 0.55$; AIC = −283.3) to BUC and SVA. However, the climate-based classifications were less efficient in explaining between-group differences in survival compared to BUC and SVA (i.e., lower R^2_m; Table 1).

A joint model including both SVA-based genetic groups and WCL-based groups (representative of the best neutral and climate-based classification, respectively)

significantly improved model fitting for both tree height and survival, as suggested by smaller AICs (Table 1). The values of R^2_m and R^2_c also suggested slightly improved fitting (Table 1). However, there was considerable population overlap between SVA-based and WCL-based groups (Figure 2c). This was indicated by good prediction of genetic groups using as a factor the WCL-based grouping ($R^2 = 0.49$; Pearson χ^2 statistic = 243.9, $p < 0.001$). It therefore suggested the presence of climate structure underlying the phylogeographic SVA classification (Appendix S1: Section S4, Table S7). Overall, the Atlantic (France, Iberia) and Eastern France–Italy neutral groups showed subhumid, cool-temperate climates and wet summers, while the Central and Eastern Iberia groups displayed a semiarid, cold climate, but with relatively wet summers. On the other hand, the southernmost groups (Morocco, Southern Iberia, and Eastern Maghreb) showed dry summers coupled with different thermal regimes (cold, temperate). When splitting the entire dataset into two subsets comprised of either consistent ($n = 63$) or conflicting ($n = 54$) populations, the mixed-effects models for tree height and survival indicated the superiority of SVA-based over WCL-based grouping (i.e., smaller AICs in the former case), regardless of subset type. Unexpectedly, this superiority was especially evident regarding tree height for the subset of conflicting populations (i.e., much lower AIC; Appendix S1: Section S4, Table S8).

Based on the aforementioned results, we considered the SVA-based classification as the arrangement of choice to delineate intraspecific patterns of phenotypic plasticity in height growth and, also, of differential survival for this species (Figure 1b). This classification had an adequate representation of genetic groups across trials, although the Eastern Maghreb and Atlantic France groups were the least represented (Figure 4; Appendix S1: Section S4, Table S9). In particular, the Eastern Maghreb group was composed of only two contrasting populations having very different thermic regimes (Data [spreadsheet format] available in Zenodo at https://doi.org/10.5281/zenodo.8079551). Also, this group has very low relevance in regard to the geographic distribution of the species, with less than 3000 km^2 of surface area (about 1% of total surface; Appendix S1: Section S1, Table S1). Therefore, we decided not to carry forward these two populations to the range-wide analysis of phenotypic plasticity.

Quantitative population genetic differentiation (Q_{ST}) for tree height calculated at the group level across trials ranged from 0.131 (Atlantic Iberia) to 0.508 (Eastern France–Italy) using a heritability value of 0.2 (Appendix S1: Section S3; Table S6). These Q_{ST} estimates were most often significantly higher than F_{ST} values

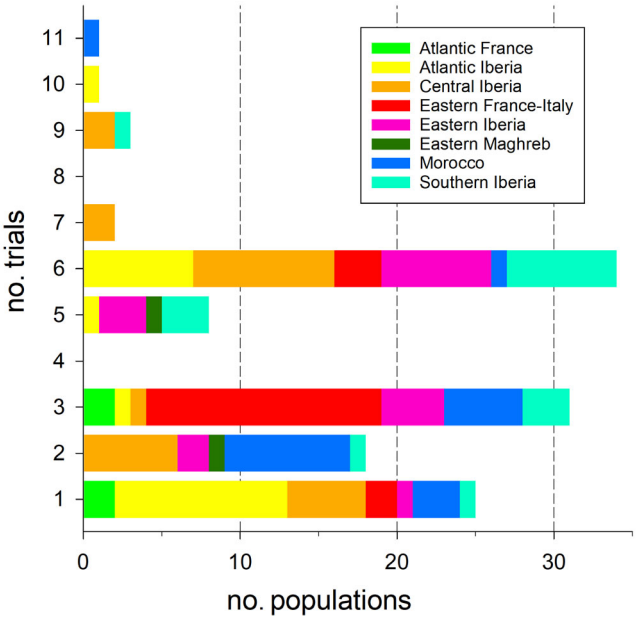

FIGURE 4 Histogram depicting the frequency distribution of the number of trials in which each population was tested in this study. The available 123 populations are classified based on the genetic groups of Serra-Varela et al. (2015).

borrowed from Rodríguez-Quilón et al. (2016) (Appendix S1: Section S3, Table S6). This result was essentially independent of the heritability value used for Q_{ST} calculation (Appendix S1: Section S4, Table S6), with the exception of the Atlantic Iberia and Moroccan groups for $h^2 = 0.5$. Q_{ST} calculated at the trial level ranged from 0.046 (Guntín) to 0.874 (Oud Lille) for a heritability value of 0.2. These estimates were significantly higher than F_{ST} values obtained at the species level for seven out of 15 trials (F_{ST} at species level = 0.099 [nuSSR] and 0.130 [SNP]; Rodríguez-Quilón et al. (2016)) regardless of the heritability value used for calculations, with few exceptions (Appendix S1: Section S4, Table S6).

Description of plasticity patterns of putatively neutral groups

Model testing and selection for the description of the plasticity of tree height is presented in Appendix S1: Section S5, Table S10. All models allowing for heterogeneity of residual trial variances provided a better fit (i.e., lower AIC) than their counterparts with homogeneous residuals. The magnitude of deviations of populations from their group mean was, thus, trial-dependent (Appendix S1: Section S5, Table S11). HRMM received the highest support (i.e., lowest AIC) among the tested models, and further evaluations were therefore based on this model. HRMM informed simultaneously on group-level

predictable (linear reaction norm slope, λ_i) and unpredictable (residual, $\sigma^2_{d_i}$) plasticity (Appendix S1: Section S5, Table S11). Specifically, the genetic group having the highest sensitivity to improving conditions (i.e., with phenotypes that change faster with the environment) was Eastern France–Italy ($\lambda = 2.658$), followed by Atlantic Iberia ($\lambda = 2.421$). Atlantic France was the group having the lowest sensitivity ($\lambda = 1.961$), followed by Morocco ($\lambda = 2.143$). The group-specific residual plasticity, $\sigma^2_{d_i}$, converged to 0 for Atlantic France, Eastern France–Italy and Eastern Iberia, suggesting highly predictable plastic effects for these groups. On the other hand, the residual plasticity was high for Atlantic Iberia, indicating large deviations from its linear reaction norm.

Model testing for survival also pointed to the superiority of models accounting for heterogeneous residuals at the trial level (Appendix S1: Section S5, Table S10). GHMM received in this case the highest support, being the model of choice for summarizing survival patterns at the group level. The neutral group displaying the highest survival variation across trials was Morocco ($\sigma^2_d = 0.021$), followed by Atlantic Iberia ($\sigma^2_d = 0.009$). Conversely, variability in survival was nil for Atlantic France, Eastern France–Italy and Eastern Iberia, pointing to stable survival across trials for these groups (Appendix S1: Section S5, Table S12).

Comparison of between-group mean differentiation and differential plasticity among putatively neutral groups

Based on the HRMM model, between-group mean differences in tree height were extremely large: a 43% relative difference was observed between extreme groups (Table 2). Atlantic France (mean = 11.1 m) and Atlantic Iberia (10.6 m) showed the largest tree height, growing significantly taller than the remaining groups (Figure 5a; Table 2). Conversely, the group having the lowest height was Morocco (8.1 m). With regard to survival, and based on the GHMM model, the range of variation was 24% in relative terms. The best surviving group was Southern Iberia (78.7%), whereas the group showing the least survival was Atlantic Iberia (63.3%) (Figure 5a). There was a negative, albeit nonsignificant, relationship between mean height and survival, suggesting a lack of sizable trade-offs between these traits at the group level (Figure 5a).

Overall, mean height growth and predictable differential plasticity, assessed through the reaction norm slope (λ_i), were unrelated at the group level (Figure 5b). By combining between-group mean differences and (predictable and unpredictable) plastic effects for height growth stemming from HRMM, we computed the probabilities of

TABLE 2 Group means and probabilities of outperformance for tree height at age 20. Means of each genetic group (SVA-based; Serra-Varela et al. [2015]) are based on a heterogeneous linear random regression mixed model (HRMM) with heterogeneous residual trial variance.

			Group i'							
Group i	Mean height (m)	LSD[a]	Atlantic France	Atlantic Iberia	Central Iberia	Eastern France-Italy	Eastern Iberia	Morocco	Southern Iberia	Mean (SD)
Atlantic France	11.14	a	...	0.64	1.00	0.99	1.00	1.00	1.00	0.94 (0.15)
Atlantic Iberia	10.64	a	0.36	...	0.87	0.83	0.87	0.96	0.86	0.81 (0.20)
Central Iberia	9.16	b	0.00	0.13	...	0.31	0.38	0.96	0.50	0.44 (0.34)
Eastern France-Italy	9.42	b	0.01	0.17	0.69	...	0.72	0.95	0.64	0.58 (0.34)
Eastern Iberia	9.23	b	0.00	0.13	0.62	0.28	...	0.96	0.55	0.49 (0.36)
Morocco	8.10	c	0.00	0.04	0.04	0.05	0.04	...	0.11	0.11 (0.20)
Southern Iberia	9.16	b	0.00	0.14	0.50	0.36	0.45	0.89	...	0.43 (0.34)

Note: The probability of i-th group (rows) outperforming the i'-th group (columns) is also shown, together with overall means and standard deviation (SD) for the outperforming probability of each genetic group.

[a]LSD, least significant difference. Different letters indicate significant differences between group means ($p < 0.05$).

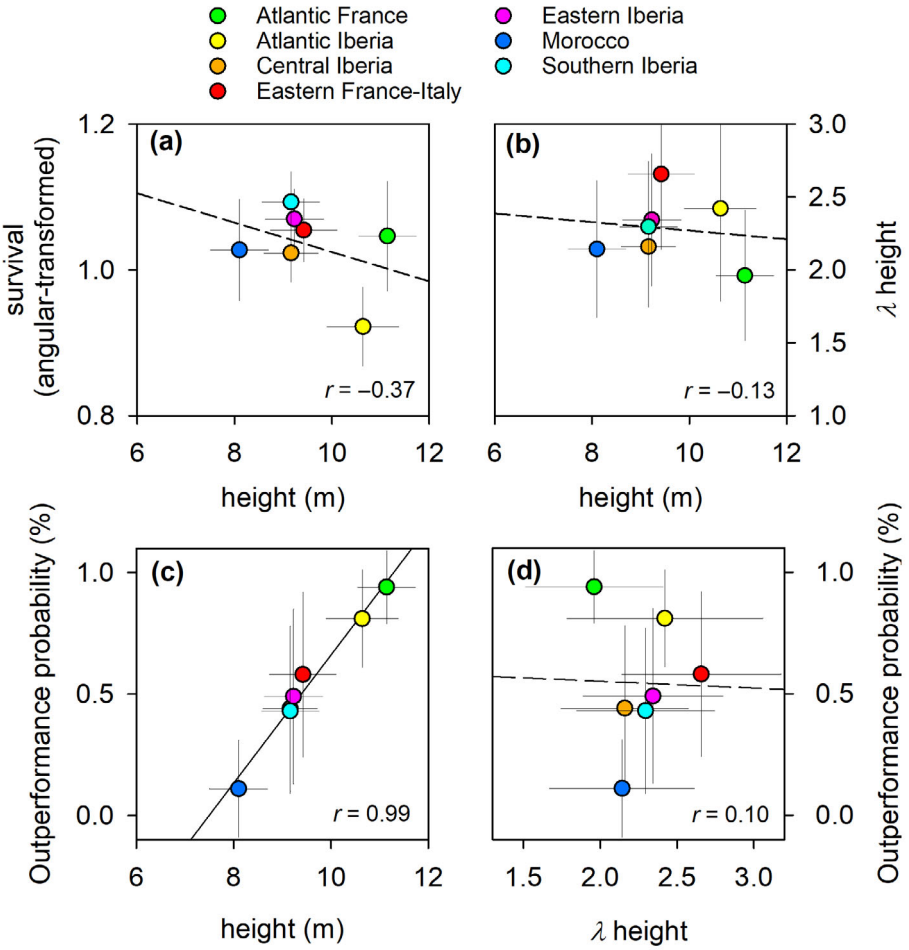

FIGURE 5 Relationships between mixed model parameters for tree height and survival. Relationships at the genetic group level (according to the assignment of populations based on Serra-Varela et al., 2015) between (a) mean tree height (according to a heterogeneous linear random regression mixed model; HRMM) and mean survival (according to a general heteroscedastic mixed model; GHMM), (b) mean tree height and sensitivity of tree height to improved environmental conditions (HRMM's λ), (c) mean tree height and probability of a given group outperforming other groups in terms of height growth, and (d) HRMM's λ and probability of a given group outperforming other groups in terms of height growth. The dot color denotes a particular genetic group following Serra-Varela et al. (2015) as shown in Figure 1b. Gray lines denote standard errors (standard deviations for probabilities of outperformance). Nonsignificant relationships are depicted with dashed lines.

a given group outperforming other groups across trials (Table 2). The group showing the largest outperforming probabilities was Atlantic France (mean across comparisons = 94%; 100% frequency of having a probability >50% of outperforming another group), followed by Atlantic Iberia (mean = 79%, outperforming in more than 50% all other groups except Atlantic France). At the lowest extreme, the Moroccan group was consistently outperformed by all other groups (mean = 5%). The remaining groups showed intermediate probabilities (between 40% and 60%).

The general patterns of height growth performance across trials generally agreed with the consistency of performance analysis carried out at the ecoregion level. For example, the superiority of materials from Atlantic areas or from the easternmost distribution of the species was confirmed in Italy, Morocco and Atlantic Spain (Figure 6a–c), denoting general adaptation. Additionally, the Central Iberia group showed consistently superior performance in central Spain regarding tree height, indicating local adaptation (Figure 6d). For survival, the local groups consistently exhibited above-average survival in their corresponding native environments (Figure 6e–h), which points toward local adaptation. Notably, the high-growth Atlantic Iberia group showed below-average survivals outside their native environments (i.e., Morocco and central Spain); conversely, a consistently poor growing group such as Morocco regularly showed good survivals, denoting in this case general adaptation and a trade-off between height growth and survival.

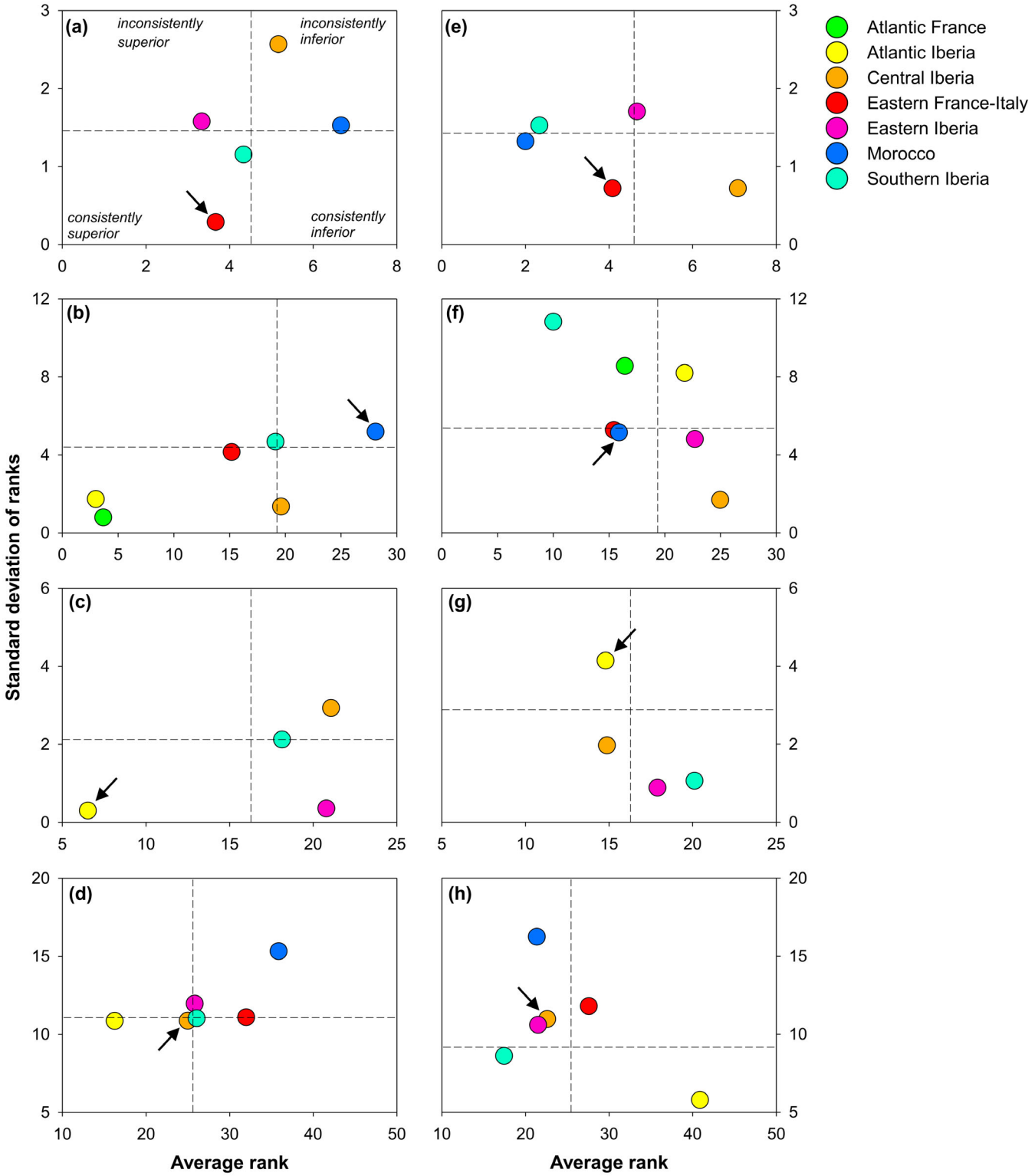

FIGURE 6 Consistency of performance analysis testing for local adaptation of tree height (left panels) and survival (right panels) at age 20. The panels show the average rank of populations for each genetic group (based on Serra-Varela et al., 2015) across trials (*X*-axis) and the standard deviation of ranks (*Y*-axis) as tested in the following ecoregions: (a, e) Italy, (b, f) Morocco, (c, g) Atlantic Spain and (d, h) Central Spain. Each panel is divided into four quadrants, one for each of the different classes in which to include the different groups, namely consistently superior, inconsistently superior, consistently inferior, and inconsistently inferior. Color coding of groups is also shown in Figure 2. Note that some groups (e.g., Atlantic France, Eastern Iberia, Eastern France–Italy) are not available in every ecoregion. The arrows indicate the native group to each ecoregion: Atlantic Iberia (for Atlantic Spain trials), Central Iberia (for central Spain trials), Eastern France–Italy (for Italian trials) and Morocco (for Moroccan trials).

The likelihood of a given group outperforming another group was tightly related to differences in group height means (Figure 5c), but not to differences in predictable plasticity (λ_i) (Figure 5d). The nonpredictable plastic component of tree height ($\sigma^2_{d_i}$) was also unrelated to the probability of outperformance (r^2 of the regression of mean probability on $\sigma^{2\prime}$s = 0.06).

DISCUSSION

Using 460 population–trial combinations from ~33,300 adult trees, we untangled the potential of *P. pinaster* populations to perform across a range-wide environmental gradient for two central adaptive traits: height growth and survival. As hypothesized, we found that intraspecific differences in these traits were concurrently explained by phylogeographic structure and adaptation to climate. In particular, we were able to summarize the species' quantitative genetic landscape through aggregated population-level models that used, as the main grouping criterion, seemingly neutral information that also incorporated a strong climatic structure. Interestingly, our range-wide evaluation indicated that between-group mean differentiation and predictable group plasticity (i.e., linear reaction norms) for height growth are unrelated in maritime pine. Although this observation may not necessarily hold at the smaller population level because finer dynamics of local evolution may come into play, they suggest independent trajectories for genetic adaptation and plasticity as modulators of trait expression at large geographical scales. We also observed a lack of predictable differential survival among groups of populations range-wide.

The relevance of phylogeography versus climate in shaping intraspecific patterns of fitness traits

For height growth, the dominance of broad (i.e., species-level) plasticity over between-group differentiation and their differential plasticity was supported by goodness-of-fit statistics (AIC, R^2_m vs. R^2_c), regardless of categorization. Such dominance is not surprising in wind-pollinated, obligately out-crossing species that span over large areas with fine-scale heterogeneous environments (Franks et al., 2014). Evaluations across fully representative conditions of the species' climate envelope, as in this study, bear the potential to unfold the actual relevance of such broad plasticity. Conversely, demographic processes and climate imprints driving between-group divergence and differential plasticity are difficult to untangle in pine species (Nadeau et al., 2016). This is particularly evident for maritime pine (Jaramillo-Correa et al., 2015).

Hence, from our range-wide analysis of tree height and survival it could be deduced that (1) the explanation of mean genetic differentiation and plastic effects slightly improved using seemingly neutral information rather than climate-based classifications of populations; (2) this improvement, although significant, was relatively minor (R^2_c-difference ≤5%), partly because broad plastic effects common to all groups dominated over between-group differentiation and their variation in plasticity; and (3) the better performance of phylogeographic over climate-based classifications was mostly due to their greater predictive ability of mean differences among groups (as shown by higher R^2_m) rather than of variation in phenotypic plasticity (as reflected in comparable R^2_c values). Albeit slight, such a superiority of phylogeographic classifications suggests that neutral structure is at least as relevant as isolation by climate as a driving factor of evolutionary divergence for these central fitness-related traits. This result gains relevance given our sampling design that maximized the exposure of populations to range-wide climatic variation (Nadeau et al., 2016).

It must be stressed, however, that the effects of phylogeography and climate on trait variation are confounded in maritime pine because of the large overlap between postglacial colonization routes and current climatic clines (Grivet et al., 2011). This is exemplified here by ~50%-population concordance between the best phylogeographic (SVA) and climate-based (WCL) classifications. In this regard, the improved model fitting of tree height and survival following the joint evaluation of genetic and climate groups points to a relevant contribution of climate-driven adaptations shaping population differentiation. This is supported by $Q_{ST} > F_{ST}$ estimates, although these statistics were obtained independently, and only for partially overlapping populations. Therefore, such direct comparison should be taken cautiously. Interestingly, Archambeau et al. (2022) recently drew a similar conclusion by combining genomics and climate into hierarchical models of height growth in a multienvironment clonal trial of maritime pine. Disentangling the genetic signatures of such climate adaptations is particularly valuable to anticipate selection responses to current warming (Archambeau et al., 2022). In this regard, we did not find evidence of such signatures—from a quantitative genetics perspective—for populations that were assigned to nondominant climate-based groups within putatively neutral groups. It may happen that climate-driven directional selection is acting at an even finer geographic scale than that afforded in our study via a representative, albeit necessarily imperfect, set of range-wide populations. For species with a

complex demographic history such as maritime pine it has been demonstrated that large-scale stabilizing selection processes may override subtler effects of directional selection shaping fitness-related traits (de Miguel et al., 2022).

Predictability versus nonpredictability of genetic effects

The range-wide multienvironment trial was instrumental in ascertaining how genetic effects (both between-group mean differences and differential plasticity) are structured in maritime pine based on quantitative variation. In particular, the variety of testing conditions matched well the array of site qualities where *P. pinaster* can be found, which ranges from ~3–12 m of height at age 20 in Spain (representing ~60% of total surface; Bravo-Oviedo et al., 2004). Also, it included an optimal site for evaluating height growth potential (A Merca, with mean height >13 m) and, even, a couple of trials representative of a warmer climate located in Morocco (cf. Figure 2a). The greatest support achieved by the HRMM model indicates that intraspecific variation in the plasticity of tree height can be adequately described by group-specific linear reaction norms to the mean phenotype (taken as environmental mean) across environments. Together with a large between-group differentiation, it suggests high predictability of genetic responses in maritime pine for height growth as compared with survival, in which genotype-by-environment interactions are best accounted for in terms of unpredictable deviations from mean group responses (i.e., GHMM model).

In spite of predictable plastic effects (i.e., distinct group-level reaction norms, λ_i), differences in mean height of ~40% among groups were largely responsible for phenotypic divergence in height growth (cf. Figure 5c,d). Whatever the underlying cause (mean population differentiation, predictable plasticity, or both), dominance of predictable adaptive-trait variation in quantitative genetics models is a desirable condition to successfully integrate genomics and environment into decision-making tools for optimal breeding and deployment strategies. This possibility has been recently explored with good prospects (Archambeau et al., 2022), and may become particularly relevant to assist forests to cope with climate change (Sork et al., 2013).

Interpreting intraspecific differentiation in tree height and survival

The adaptive relevance of growth traits for maritime pine has been confirmed in genomic studies through comparison of F_{ST} and Q_{ST} indices (González-Martínez et al., 2002; de Miguel et al., 2022; Rodríguez-Quilón et al., 2016; this work), identification of candidate genes (Jaramillo-Correa et al., 2015), or gene–environment associations (Grivet et al., 2011; Serra-Varela et al., 2015). From a quantitative genetics perspective, the importance of tree height as a fitness-related trait has been corroborated through the analysis of plastic effects as related to climate factors at the origin of populations (Alía et al., 1997) or the identification of evolutionary trade-offs involving for example, insect resistance (Di Matteo & Voltas, 2016). Markedly, the variation in tree height found in our study among seemingly neutral groups agrees, to a large extent, with expected patterns of climate adaptation for the species. For example, those groups mainly from (i.e., likely adapted to) nonwater-limiting areas (Atlantic France and Atlantic Iberian Peninsula) showed the highest tree height, which is consistent with the need to overtop and outcompete neighboring individuals of the same or other species for nutrients and light. On the other hand, groups occupying drought-prone areas (e.g., Southern Iberia, Morocco) grew significantly shorter. Previously reported differences among populations in root morphology, whole-plant conductance, carbon allocation, plant growth and water-use efficiency are consistent with this pattern of variation, with xeric populations often exhibiting lower growth, higher investment in roots and conservative water use (Aranda et al., 2010; Corcuera et al., 2012). While our range-wide results reaffirm the relevance of neutral processes as drivers of the evolutionary history of maritime pine, as suggested by major fitness-related traits such as height growth and survival, they also hint at an important role of climate-induced local adaptation in shaping intraspecific differentiation for the species (Grivet et al., 2011). This seems particularly evident for populations from drought-prone areas (i.e., Morocco), which exhibited high range-wide survival in low-density planted genetic trials likely as a result of their conservative resource use strategy.

As a likely factor involved in the evolutionary process of adaptation, we quantified the role of differential plasticity modulating height growth expression of adult maritime pine trees. With the exception of Atlantic France, highly reactive groups to improved conditions tended to show a higher probability of outperforming other groups (cf. Figure 5d), which can be interpreted as a better competitive ability under favorable conditions. The limited height growth plasticity of groups/populations mainly originating from stressful (i.e., drought-prone) environments may indicate increased levels of phenotypic integration (i.e., trade-offs with other traits such as reproduction; Santos-del-Blanco et al., 2013) and increased costs of

plasticity under stress (Valladares et al., 2007). The genetic groups of Atlantic France and Atlantic Iberia would deserve further attention because their performance denotes general adaptation (i.e., they exhibit consistently superior mean height growth), although in the case of Atlantic France this realization may be hampered by the imperfect evaluation of populations of this group across trials. Anyhow, it is consistent with the observation that populations from this gene pool show great responsiveness and adjustment to drought conditions (i.e., similar embolism resistance to dry populations), in addition to high growth (Corcuera et al., 2011). This is indeed confirmed here by the above-average survival of this group under the suboptimal conditions encountered in the Moroccan trials (cf. Figure 6f).

Results also indicated that the mean likelihood of survival was variable at the group level and essentially independent of mean height growth. Therefore, this finding is not supportive of a general adaptive syndrome for maritime pine by which less reactive groups to ameliorated (e.g., nonwater-limited) conditions should show higher survival rates coupled with lower growth (Valladares et al., 2007). A clear exception would be the Moroccan group of populations. Overall, however, these results are in concord with the outcome of a recent meta-analysis involving Mediterranean forest species (Ramírez-Valiente et al., 2022). The strong legacy of demographic effects on the genetic structure of maritime pine likely underlies this finding.

In conclusion, by broadening the scope of inferences to the most current growing conditions for maritime pine, which also included some trials representative of a warmer climate, we showed at least as high relevance of phylogeography as that of climate shaping the quantitative genetic landscape of a widespread conifer. This observation may partly explain the lack of generalized trade-offs between height growth and survival found in this study. Our analysis also suggests potentially different mechanisms of intraspecific adaptation involving genetic divergence and phenotypic plasticity acting under global change. The analytical framework presented here can be useful to guide future works aimed at disentangling plasticity and genetic differentiation explaining phenotypic divergence in range-wide studies of fitness-related traits, and simultaneously provide hints for optimized use of genetic material of Mediterranean pines, both at commercial level (e.g., assisted migration; Benito-Garzón & Fernández-Manjarrés, 2015) and for genetic resources conservation (Lefèvre et al., 2013; Rodríguez-Quilón et al., 2016).

AUTHOR CONTRIBUTIONS

Jordi Voltas and Rafael Zas conceived and designed the research. Ramon Amigó, Giovanni di Matteo, Raquel Díaz and Rafael Zas collected the data. Jordi Voltas, Ramon Amigó and Tatiana A. Shestakova analyzed the data. Jordi Voltas wrote the manuscript, with contributions from Ramon Amigó, Tatiana A. Shestakova, Giovanni di Matteo, Raquel Díaz and Rafael Zas.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Voltas et al., 2023) supporting the results of this study are available in the CORA open repository at https://doi.org/10.34810/data871. Data (Voltas, 2023) describing the characteristics of populations are available in Zenodo at https://doi.org/10.5281/zenodo.8079551.

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SUPPORTING INFORMATION

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

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