Ecotypic variation and stability in growth performance of the thermophilic conifer *Pinus halepensis* across the Mediterranean basin

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ABSTRACT

The combined effects of local adaptation and phenotypic plasticity influencing plant performance are relevant to understand the capacity for genetic responses to climate change. *Pinus halepensis* is a native species of low- to mid-elevation Mediterranean forests with a high ecological value in drought-prone areas. Thus, it is of utmost importance to determine its adaptive structure for key traits such as growth or survival. Here, we analyse a highly unbalanced dataset collated from different common-garden networks that cover the distribution range of the species. A total of 82 range-wide populations were evaluated in nine Mediterranean trials located in Israel, Italy and Spain. A climate classification of populations allowed for the definition of six different groups, or ecotypes, which showed contrasting performances for tree height and survival at age 15. The effects of ecotypic differentiation and among-ecotypes genetic variation in plasticity were disentangled by fitting stability models accounting for interaction and heteroscedasticity in genotype-by-environment tables. For growth, a Finlay–Wilkinson model suggested high predictability of ecotypic plastic responses in *P. halepensis*, as described by different linear reaction norms. However, differences in mean height of *ca.* 15% among ecotypes dominated intra-specific patterns of tree growth across trials, pointing to preponderance of genotypic adaptation over differential ecotypic plasticity in this species. For survival, ecotypic differences were approximately constant across trials, suggesting lack of genotype-by-environment effects. Sub-humid cool climate populations from the eastern Mediterranean (e.g., Greek populations) showed general adaptation and high sensitivity to improved growing conditions, as opposed to populations from the driest ecological extreme of the species (e.g., south Spain and Maghreb populations), which exhibited specific adaptation to harsh environments. Altogether, our results indicate a general adaptive syndrome by which less reactive ecotypes to ameliorated conditions (e.g., non-water-limited) would be associated with high survival rates and low growth. The reported ecotypic differentiation constitutes the basis for tailoring intra-specific responses to climate and disentangling the relationship between adaptive variation and resilience towards climatic warming for this exemplary Mediterranean pine.

1. Introduction

Mediterranean forests in a changing climate are exposed to the unpredictability of the timing and intensity of drought as most restrictive factor for plant performance. Besides, the combination of additional abiotic factors (e.g., low nutrient availability, low winter temperature), biotic threats (e.g., pest outbreaks, diseases) and perturbations (e.g., fire) involves functional trade-offs and imposes conflicting selective pressures on plants (Valladares, 2008). To cope with this array of conditions, plant species can adjust to the environment through local adaptation or through phenotypic plasticity. Local adaptation implies a shift in allele frequencies leading to a change in phenotype in a population (i.e., genetic differentiation), whereas phenotypic plasticity is defined as the range of phenotypes that a single genotype can express as a function of its environment (Conner and Hartl, 2004). Phenotypic plasticity and local adaptation have been long proposed as partially independent mechanisms shaping plants' responses to the environment (Nicotra, 2010). In evolutionary genetics, the relative contributions of genetic change and plasticity in determining phenotypic responses to the environment remain largely unknown (Merilä and Hendry, 2014). In particular, information for Mediterranean plants is still insufficient on the constraints to plasticity,

its adaptive value and its transgenerational potential, and also on the adjustment of genetic change to environmental change (Matesanz and Valladares, 2014).

From a quantitative genetics perspective, differences in phenotypic plasticity among genotypes can be assessed through the analysis of genotype-by-environment (GE) interaction. GE interaction is defined as the difference in the response of genotypes to different environments (Bradshaw, 1965). Multi-environment trials (MET) are fundamental for understanding GE interactions, but they are relatively scarce in the case of forest species, mainly due to the difficulties posed by the long rotation periods and the management of trials. However, differences in phenotypic plasticity linked to sizeable GE interactions have been reported for growth responses involving provenances of pines (di Matteo and Voltas, 2016; Sierra-Lucero et al., 2002), Norway spruce clones (Isik and Kleinschmit, 2003) or hybrid poplars (Sixto et al., 2014), among others. An extensive collection of approaches exists for studying GE interaction (Romagosa and Fox, 1993; Piepho and van Eeuwijk, 2002). In this regard, mixed models provide a suitable framework for assessing GE interaction and interpreting plasticity in terms of genotypic stability (reviewed in Piepho and van Eeuwijk, 2002). The concept of genotypic stability is regarded, from an agronomic perspective, as the genotype's capacity to perform according to the productive potential of each environment (Becker and Leon, 1988). Most stability measures can be embedded in a mixed-model framework through modelling of variance–covariance structures, where environments are a random factor and genotypes a fixed factor (Denis et al., 1997). By using an appropriate stability model, accurate inferences on mean responses underlying genetic changes can also be drawn, hence providing comprehensive information on genetic differentiation (potentially linked to local adaptation) and variation in the stability of responses (linked to phenotypic plasticity) among genetic entities.

The circum-Mediterranean conifer Aleppo pine (*Pinus halepensis* Mill.) is the most widely distributed tree species in the Mediterranean basin. It shows an extensive ecological breadth and is seemingly adapted to a broad range of abiotic stressors and perturbations, especially fire and drought (Ne'eman et al., 2004; Schiller and Atzmon, 2009; Klein et al., 2011, 2016). *P. halepensis* is also extensively used in afforestation programs in the region. Previous studies performed in common-garden tests or under controlled conditions revealed ecotypic differentiation and high phenotypic plasticity for functionally important traits, such as biomass allocation (Chambel et al., 2007; Climent et al., 2008), access to soil water pools (Voltas et al., 2015), wood anatomy (Esteban et al., 2010) and vulnerability to xylem embolism (Klein et al., 2013; David-Schwartz et al., 2016). Overall, these studies demonstrate that populations dwelling in dry environments exhibit different characteristics from their counterparts originating from mesic areas, hence revealing complex anatomical, morphological and physiological adjustments and adaptations at the intra-specific level.

The relative amount of phenotypic variation explained by plasticity vs. genetic differentiation is contingent on the climatic range of the sampled individuals and the environments they inhabit as well as the climatic range of test sites (Franks et al., 2014). For understanding tree performance, a comprehensive investigation of phenotypic variation in *P. halepensis* for a key trait such as tree height is lacking across the Mediterranean basin. The few available studies aimed at disentangling the effects of phenotypic plasticity and local adaptation on tree growth involved a few populations and incomplete testing conditions (e.g., Baquedano et al., 2008; Santos del Blanco et al., 2013; Taïbi et al., 2015). The only comprehensive analysis of phenotypic variation in *P. halepensis* made use of an extensive tree-ring network obtained across the Mediterranean basin (de Luis et al., 2013) and showed substantial plasticity of the species in response to different climate conditions. The study by de Luis et al. (2013) pointed to climate variability as the fundamental player shaping the adaptive structure of *P. halepensis*, as has also been anticipated in common-garden studies for a number of functional traits including growth (Climent et al., 2008; Voltas et al.,

2008). However, the source of response variability in tree growth as being due to population differentiation, phenotypic plasticity, or both factors acting together remains basically unsolved.

In this study, we use a broad trial network in which range-wide *P. halepensis* populations are evaluated in the western, central and eastern areas of the species distribution, thus being the first comprehensive work that disentangles the effects of ecotypic differentiation and among-ecotypes genetic variation in plasticity on growth across the entire Mediterranean basin. In particular, a total of 82 populations have been evaluated for tree height and survival at age 15 in nine field trials located in Israel, Italy and Spain. The main aim of this study is to characterise the adaptive performance of Aleppo pine ecotypes regarding growth and survival at maturity. Specifically, we aim at assessing and interpreting possible differences in ecotypic stability for the growth of the material tested. We hypothesize that populations originating from stressful (i.e., drought-prone) environments will show limited plasticity in growth, owing to increased levels of phenotypic integration (i.e., trade-offs with other traits such as reproduction; Santos del Blanco et al., 2013) and the increased costs of plasticity under stress (Valladares et al., 2007), as opposed to populations found in mesic sites. The results will be valuable to understand better future species' performance with regard to climate change considering the relevance of local adaptation and intra-specific variation in plastic responses for growth. Eventually, this study could also assist with a proper deployment of genetic material in management practices (e.g., afforestation, assisted migration) in which either productivity and carbon sequestration or promotion of forest adaptation to climate change may be of particular relevance.

2. Materials and methods

2.1. Plant material

Seed sources from 82 populations of Aleppo pine (*Pinus halepensis* Mill.) were used representing most of the natural distribution range of the species, which spans the Mediterranean basin (Fig. 1). The populations originated from mainland Spain (42 populations), the Balearic Islands (9), France (1), Italy (7), Greece (8), Lebanon (1), Israel (2), Tunisia (5), Algeria (3) and Morocco (4) (Suppl. Table S1). For each population, climatic variables at origin were obtained for the period 1960–1990 from two different databases that provided climate estimates with different spatial resolution: the CRU dataset (Climatic Research Unit, CRU TS 3.24; Harris et al., 2014) and the WorldClim database (Global Climatic Data, WorldClim v. 1.4; Hijmans et al., 2005). CRU delivers climate series available on a coarse resolution (0.5° × 0.5° grid-box basis), interpolated from meteorological stations across the globe, and climate information for each population was retrieved from the nearest grid point. WorldClim, alternatively, provides high-resolution estimates of local climate with a spatial resolution of 1 km². In both cases, the climatic variables were chosen based on previous identification of climate drivers of ecotypic variation in Mediterranean pines (Tapias et al., 2004; Climent et al., 2008) 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).

2.2. Study sites and field measurements

Provenance trials were available at nine locations distributed across the Mediterranean basin (Fig. 1). Six trials were established within the framework of the FAO/Silva Mediterranean international initiative (Chambel et al., 2013). These are three trials from Italy planted in 1976 (Castel di Guido and Ovile, Rome province; Castiglioncello, Grosseto province) and three trials from Israel planted in 1985 (Bet Dagan, Center District; Yatir East and Yatir West, Negev desert). The remaining
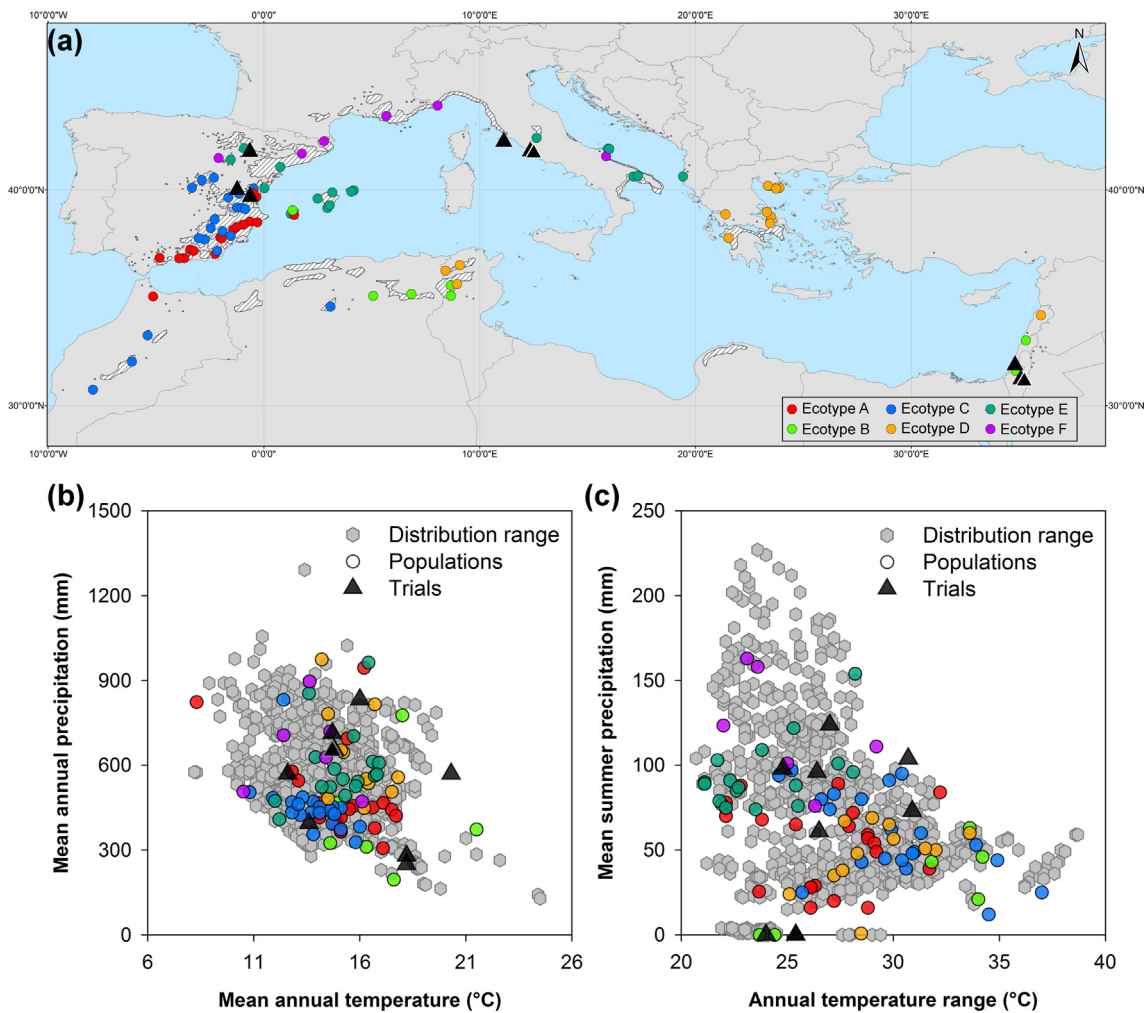
Fig. 1. (a) Distribution range of *P. halepensis* identified with hatching. Populations evaluated in the multi-environment trial are shown with dots and trials with black triangles. The dot colour denotes a particular ecotype as identified in the dendrogram of Fig. 2. (b and c) Autoecology diagrams of *P. halepensis* distribution based on WorldClim data (resolution = 10′) with trials depicted as black triangles and populations depicted as coloured circles. The species range is derived from the EUFORGEN distribution map (http://www.euforgen.org/species/pinus-halepensis). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Geographic and climatic characteristics of the nine provenance trials used in this study. Climate data were obtained from WorldClim (Hijmans et al., 2005).

Trial	Latitude	Longitude	Altitude (m)	MAT (°C)	TAR (°C)	MAP (mm)	MSP (mm)	Soil texture
Israel								
Bet Dagan	31°59′N	34°49′E	60	19.5	24.0	573	0	Sandy-loam
Yatir East	31°20′N	35°05′E	700	17.4	25.4	307	0	Sandy-clay
Yatir West	31°21′N	35°02′E	650	18.3	25.4	291	0	Sandy-clay
Italy								
Castel di Guido	41°53′N	12°27′E	40	15.6	26.5	728	61	Clay
Castiglioncello	42°21′N	11°07′E	225	14.2	24.8	644	98	Sandy-clay
Ovile	41°54′N	12°22′E	60	15.6	26.4	757	96	Sandy-clay
Spain								
Ademuz	40°03′N	01°17′W	850	11.1	30.7	477	104	Clay-loam
Altura	39°49′N	00°34′W	640	14.0	27.0	468	124	Clay-loam
Vedado de Zuera	41°52′N	00°38′W	350	12.7	30.9	423	73	Loamy

MAT = mean annual temperature; TAR = temperature annual range; MAP = mean annual precipitation; MSP = mean summer precipitation (June to August).

three trials were established in Spain in 1998 (Ademuz, Valencia province; Altura, Castellón province; Vedado de Zuera, Zaragoza province) and are maintained by the Spanish network of forest genetic trials (GENFORED). Geographic and climatic details of the trials are provided in Table 1. Not all populations were tested at every field trial; in fact, the dataset was extremely unbalanced, reflecting the different age,

objectives and resource availability of each experiment. Most populations (71%) were evaluated just in three trials by the characteristics of the trial network, which were conditional to the preferences of each country, including also differences related to trial layout, planting density and number of trees per population. Six populations were only tested at one trial (Aures Beni Melloum, Algeria; María, mainland

Spain; Montmell, mainland Spain; Ouarsenis, Algeria; Oum Djeddour, Algeria; Zaouia Ifrane, Morocco). Conversely, four populations (Elea, Greece; Elkosh, Israel; Eubeoa, Greece; Vico del Gargano, Italy) were evaluated in six trials and one population (Otricoli, Italy) was evaluated in seven trials. In summary, out of the 738 potential population–trial combinations only 248 were available (34%). This data structure can be considered as typical situation in transnational multi-environment forest genetic trials (Chambel et al., 2013). However, all trials had a good representation of populations covering the circum-Mediterranean distribution of the species. The general features of the experimental set-up at each trial are provided in Suppl. Table S2.

Total height was used as an indicator of population and site differences in productivity (Skovsgaard and Vanclay, 2007) and was measured in most trees of each population every 1–5 years depending on the trial. In Israel, height measurements were available at ages 11 and 18, except for Yatir West, which had records available at age 20 instead of age 18. In Italy, height measurements were available at age 15, except for Castglioncello, which had records available at ages 5, 8 and 10. In Spain, height measurements were available at age 14. Additionally, results on tree survival were available for the same ages reported for tree height. They were expressed as the percentage of living trees per population at the trial level.

2.3. Age adjustments of tree height

For each population, an estimate of mean tree height at age 15 was obtained for each trial as follows. First, best linear unbiased estimators of population means were obtained wherever individual tree (i.e., raw) records were available. This was the case for the Spanish trials, in which a linear mixed-effects model was fitted accounting for the Latinised row–column design implemented at each experimental set-up. Here, the low range of plot error variances at the trial level indicated that genotype-treatment means were measured with approximately equal precision. For the remaining trials, original records were not available (these trials reached age 15 in 1991 and 2000 for Italy and Israel, respectively) and population means were used instead. Second, for those trials in which height at age 15 was not measured, population means available at different ages were linearly interpolated (Israel) or extrapolated (Castglioncello and Spanish trials) to obtain 15-year estimates. This approach assumed linear increases in tree height from ages 8 to 20 (i.e., at adult stage), as has been previously reported for the species (Montero et al., 2001). The methodology performed well when tested in the Yatir East dataset with 1-, 8-, 11- and 18-year values ($r^2 = 0.79$–0.97, with $r^2 > 0.90$ for 16 out of 19 provenances). For tree survival, we used results from the nearest age to the target age of 15 years when this evaluation was carried out. In this case, we did not perform any age adjustment since changes in survival rates at ages over ten years were negligible (results not shown).

Differences in planting density among trials (Table 1) were considered irrelevant for primary growth at age 15 (Lanner, 1985), as it has been demonstrated for the taxonomically close Mediterranean conifer *Pinus brutia* at age 12 (Erkan and Aydin, 2016). Therefore, any correction for density effects was deemed unnecessary when analysing the complete trial network for stability of height responses (see Section 2.5.2).

2.4. Grouping of provenances into ecotypes

Hierarchical cluster analysis (Ward's method; Ward, 1963) was used to identify genetic units (or ecotypes) with potentially divergent adaptive characteristics triggered by climate. To this end, each population was assigned to a different group based on climatic information at origin using either CRU (coarse resolution) or WorldClim (high resolution) data. Climate variables used were MAT, MAP, TAR and MSP. The inclusion of two additional variables (TMX, TMN) did not modify substantially the resulting classifications (results not shown). The

resulting ecotypes were given a particular climate type based on three criteria following Le Houérou (2004): (i) summer precipitation (low, MSP ≤ 60 mm; medium–high, MSP ≥ 80 mm), (ii) winter temperature (cold, −1 < TMN ≤ 1 °C; cool, 1 < TMN ≤ 3 °C; temperate, 3 < TMN ≤ 5 °C) and (iii) annual precipitation (arid, MAP ≤ 400 mm; semiarid, 400 < MAP ≤ 600; sub-humid, MAP > 600).

2.5. Data analysis

2.5.1. Linear fixed-effects model

As first exploratory analysis height and survival data were subjected to standard analysis of variance (ANOVA) with fixed effects for ecotype, population nested to ecotype, trial and ecotype by trial interaction as follows:

$$Y_{ijk} = \mu + T_k + E_i + P(E)_{ij} + (ET)_{ik} + e_{ijk} \qquad (1)$$

where Y_{ijk} is the observation of the jth population of the ith ecotype in the kth trial, μ is the general mean, T_k is the effect of the kth trial, E_i is the effect of the ith ecotype, $P(E)_{ij}$ is the effect of the jth population nested to the ith ecotype, $(ET)_{ik}$ is the effect of interaction between the ith ecotype and the kth trial, and e_{ijk} is the random residual effect of the interaction between the jth population nested to the ith ecotype and the kth trial. In this way, the total population by trial interaction was partitioned into ecotype by trial effects plus a population by trial residual. Type I (sequential) sum of squares was used for hypothesis testing (Nelder, 1994). In this way, genotypic effects (ecotypes and populations nested to ecotypes) were previously adjusted for trials following Eq. (1). Prior to analysis, survival rates per population-trial combination (mostly ranging between 30 and 100%) were angular-transformed (arcsin square root transformation) to stabilize variances (Bowley, 1999).

2.5.2. Mixed-effects models for analysis of ecotypic stability

A number of mixed models accounting for interaction and heteroscedasticity in genotype-by-environment tables were tested for height and survival data. These are generalizations of common stability measures useful for describing genotype-by-environment interactions that can be readily embedded in a mixed-model framework (Denis et al., 1997; Piepho, 1999). All these models considered ecotype as fixed effect, and population nested to ecotype, trial, and ecotype by trial interaction as random effects. A theoretical justification for this choice is that we were interested in characterising the performance of a set of ecotypes and not concerned about the trials themselves, which represent random variation drawn from the entire population of trials; indeed the trials (i.e., environments) were only considered to provide information about ecotypic differences. Two different sets of stability models were fitted: (i) assuming homogeneity of residual variances across trials (i.e., uniform deviations of populations from ecotype means across trials plus uniform deviations of population means across replicates within each trial) or (ii) allowing for heterogeneity of residual variances among trials (i.e., trial-specific deviations of populations from ecotype means plus trial-specific deviations of replicates from population means).

Here we followed the framework proposed in Denis et al. (1997), which represents a unified approach by which mixed models of our multi-trial data can be expressed and compared. Each model is outlined 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 sensible. In particular, the main term of interest here is $(ET)_{ik}$ as defined in Eq. (1), which represents ecotype-by-trial effects. This part can be modelled in a very flexible way (Denis et al., 1997), and classical stability approaches for describing such effects were handled using appropriate variance-covariance (VCOV) structures as follows.

The general forms of expectation (ε) and variance in our mixed model variants of Eq. (1) are:

$$\varepsilon(Y_{ij}) = \alpha_i; \text{var}(Y_j) = \sigma_{P(E)}^2 + \sigma_T^2 + \Gamma + \sigma_e^2 \quad (2)$$

where α_i refers to the ith ecotype main effect and $\sigma_{P(E)}^2$, σ_T^2, and σ_e^2 are the population nested to ecotype variance, the trial variance and the error variance respectively. The term Γ defines a particular VCOV structure used to model the random term of interest $(ET)_{ik}$. Four different VCOV structures which represent five stability measures were fitted to ecotype-by-trial effects:

(1) Simple (R₁): $\quad \text{cov}(ET_{ik}; ET_{ik^*}) = \sigma_{ET}^2$ when $k = k^*$, otherwise $\text{cov}(ET_{ik}; ET_{ik^*}) = 0$.

(2) Diagonal (R₂): $\quad \text{cov}(ET_{ik}; ET_{ik^*}) = \sigma_{ET_i}^2$ when $k = k^*$, otherwise $\text{cov}(ET_{ik}; ET_{ik^*}) = 0$.

(3) Factor analytic 1 (R₃): $\quad \text{cov}(ET_{ik}; ET_{ik^*}) = \lambda_{1k}\lambda_{1k^*} + \sigma_d^2$ when $k = k^*$, otherwise $\text{cov}(ET_{ik}; ET_{ik^*}) = \lambda_{1k}\lambda_{1k^*}$.

Where λ_{1k} and λ_{1k^*} are environment-specific multiplicative parameters and σ_d^2 is a common residual variance (Piepho, 1997).

(4) Factor analytic 1 + heterogeneity (R₄): $\quad \text{cov}(ET_{ik}; ET_{ik^*}) = \lambda_{1k}\lambda_{1k^*} + \sigma_{d_k}^2$ when $k = k^*$, otherwise $\text{cov}(ET_{ik}; ET_{ik^*}) = \lambda_{1k}\lambda_{1k^*}$.

Where $\sigma_{d_k}^2$ accounts for a residual heterogeneity (i.e., environment-specific deviation) (Piepho, 1997).

The stability models were as follows:

Model 1 (additive mixed-effects model). This is the simplest model in which the variance takes the form:

$$\text{var}(Y_{ij}) = \sigma_{P(E)}^2 + \sigma_T^2 + R_1 + \sigma_e^2 \quad (3)$$

where $\sigma_{P(E)}^2$, σ_T^2, σ_e^2 and R₁ are defined as above. According to this model the ecotypes do not differ in stability. The number of variance components equals four in our particular case.

Model 2 (general heteroscedastic model). This model extends the additive model by attributing a different variance component (or stability measure) to each ecotype:

$$\text{var}(Y_{ij}) = \sigma_{P(E)}^2 + \sigma_T^2 + R_2 + \sigma_e^2 \quad (4)$$

This model, also known as Shukla's stability variance (Shukla, 1972), has $I + 3$ variance components.

Model 3 (Finlay–Wilkinson regression). This is the mixed model version of the widespread Finlay–Wilkinson (F–W) regression on the environmental mean (Finlay and Wilkinson, 1963), which may be fitted using a simplified factor analytic structure with one factor:

$$\text{var}(Y_{ij}) = \sigma_{P(E)}^2 + R_3 + \sigma_e^2 \quad (5)$$

In this case, the trial variance component σ_T^2 is dropped from the modelled variance–covariance structure underlying the response variable Y_{ij}. This structure is over-parameterised and therefore an identifiability constraint needs to be imposed. Here we used the constraint $\sigma_w^2 = 1$, as ecotypic λ_i's in R₃ represent sensitivities to a hypothetical underlying variable w_j (Piepho, 1997; Piepho, 1999). Whatever the constraint used, however, the relative magnitude of the values of λ_i's indicates the sensitivity to unobservable environmental conditions as measured by the environmental means (Piepho, 1998), which can also be interpreted in terms of the reaction norm slope as applied in evolutionary biology (Chevin et al., 2013). The number of variance components is $I + 3$.

Model 4 (Eberhart–Russell regression). This is the mixed model equivalent of the Eberhart–Russell stability model (Eberhart and Russell, 1966), which extends the F–W regression to allow for heterogeneity in interaction variances. It can be fitted using a complete factor

analytic VCOV structure with one factor:

$$\text{var}(Y_{ij}) = \sigma_{P(E)}^2 + R_4 + \sigma_e^2 \quad (6)$$

As in Model 3, the environmental variance component σ_T^2 is dropped from the modelled variance and an identifiability constraint needs to be imposed. The interpretation of λ_i's is identical to the F–W model. The number of variance components is $2I + 2$.

Model 5 (AMMI–1 model). This is the mixed model version of the additive main effects and multiplicative interaction model with one multiplicative component (Kempton, 1984). As for the previous model 3, it can also be fitted using a complete factor analytic VCOV structure with one factor. In this case, however, the trial variance component σ_T^2 is retained for modelling purposes as follows:

$$\text{var}(Y_{ij}) = \sigma_{P(E)}^2 + \sigma_T^2 + R_3 + \sigma_e^2 \quad (7)$$

Here, λ_{1k}, as defined in R₃, is the factor loading associated with a particular ecotype, which can be interpreted as the sensitivity of this ecotype to the value of a hypothetical environmental variable (or factor score) for trial j (Piepho, 1997; Smith et al., 2002).

The adequacy of different VCOV models was compared by computing the restricted log-likelihood for each model and deriving information criteria such as Akaike's information criterion (AIC) and Bayesian information criterion (BIC). Both involve a penalty for the number of parameters in the VCOV structure, which favours parsimonious models, but BIC penalizes a large number of parameters more strongly than does AIC. Both statistics are in the smaller-is-better form. Multiple mean comparisons among the ecotypes across trials for the best fitting models (for height and survival) were performed using a Fisher's least significant difference (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 ecotypes accounting for the variance–covariance model selected.

The analyses were performed using the MIXED procedure of SAS/STAT (Littell et al., 1996).

2.5.3. Consistency of performance analysis

We also evaluated the potential joint effects on tree height of varying trial density, soil and climate conditions among regions (countries) by carrying out a consistency of performance analysis (Ketata et al. 1989). This analysis is based on the simultaneous use of the average height rank across environments and its standard deviation for each population. These two variables allow for the relative classification of populations (ecotypes) into four different classes: (1) populations showing high ranks and low standard deviation of ranks (class of consistently superior populations); (2) populations showing high ranks but also high standard deviation of ranks (class of inconsistently superior populations); (3) populations showing low ranks and low standard deviation of ranks (class of consistently inferior populations); and (4) populations showing low ranks but high standard deviation of ranks (class of inconsistently inferior genotypes). The analysis was performed independently for trials of Israel, Italy and Spain. In this way, we sought to clarify whether the overall conclusions of the range-wide stability analysis held true across broad Mediterranean regions given the large unbalancedness of the dataset.

2.5.4. Probability of a particular ecotype outperforming another ecotype

The analysis of ecotypic stability of tree height, as outlined in Section 2.5.2, characterises stability regarding some measure of variation, but it is desirable to complement this measure with the mean ecotypic value (i.e., standing genetic variation) to better understand the relative superiority or otherwise of the material under evaluation (Piepho, 1998). Accordingly, the concept of genotypic stability can be reassessed by the joint examination of the mean and variability of ecotypic growth. In this framework, the risk of poor performance can be
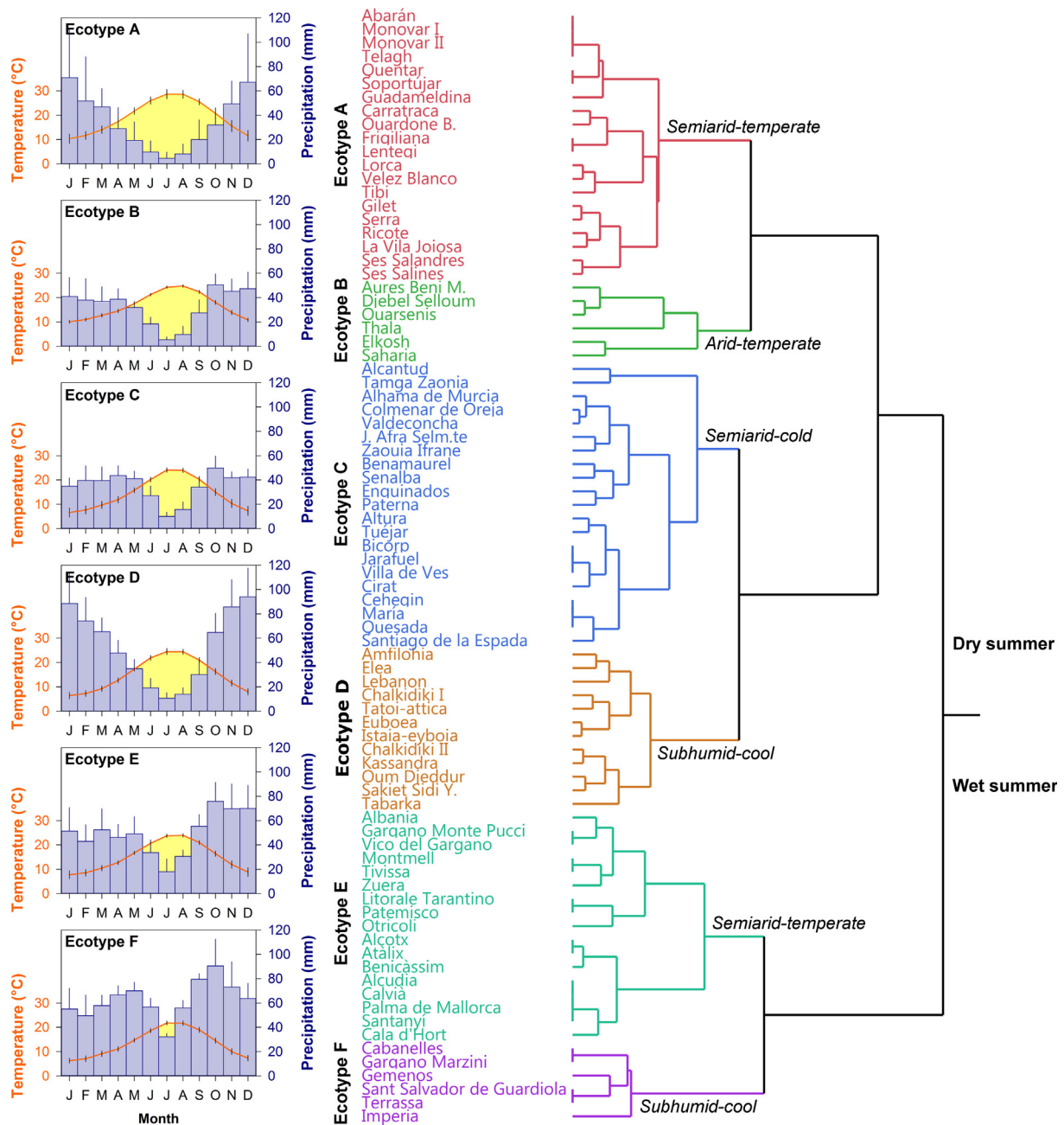
Fig. 2. Dendrogram of the classification of *P. halepensis* populations into ecotypes according to climate (CRU-based classification). The climate characteristics of each ecotype are succinctly described in the dendrogram following Le Houérou (2004) and are shown in detail by climographs (left panels), where the average monthly values of populations at origin (and their standard deviation across populations) are indicated. The area of the climographs in yellow indicates the drought period, that is, the period when mean monthly temperature exceeds twice the amount of total precipitation.

evaluated in terms of the probability of one ecotype outperforming another ecotype (Eskridge and Mumm, 1992). Briefly, this probability can be computed as

$$\Pr(D_j > 0) = \Phi[\partial/\sigma_D] \qquad (8)$$

where D_j is the difference of productivity between ecotype 1 and ecotype 2 in trial j, Φ is the cumulative distribution function of the standard normal distribution, $\delta = \mu_1 - \mu_2$, and σ_D^2 is the variance of a difference D_j in a randomly chosen environment. For model 3 (Finlay–Wilkinson regression), this variance equals (Piepho, 1998):

$$\sigma_D^2 = (\lambda_1 - \lambda_2)^2 \sigma_w^2 + \sigma_d^2 \qquad (9)$$

3. Results

3.1. Cluster assignment of populations to ecotypes

The cluster analysis produced six distinct groups of populations (i.e., ecotypes) using either CRU (Fig. 2) or WorldClim (Suppl. Fig. S1) as climate source for population classification. The CRU-based grouping captured 69% of the total variability of climate records (MAT, MAP, TAR, and MSP), whereas the WorldClim-based grouping explained 64% of the total variability. In addition to greater separation among clusters, the CRU classification also accounted for a markedly higher percentage of tree height differences among populations than the alternative WorldClim grouping (see Section 3.2). As a consequence, we chose the CRU-based population grouping for subsequent analyses of ecotypic

stability. The mean climate characteristics of these groups (i.e., ecotypes) are presented in Suppl. Table S3. The most important climatic variables accounting for ecotypic differentiation were May–June temperature and August–September precipitation. However, all monthly variables were relevant to explain ecotypic differences (Suppl. Fig. S2).

Two main groups of ecotypes could be distinguished (Fig. 2) which differed markedly in summer precipitation: low MSP (53 mm or less) and medium-high MSP (83 mm or more). The low MSP group included (i) ecotypes typical of warm areas having temperate winters and an arid (ecotype A) or a semiarid (ecotype B) climate and (ii) ecotypes from colder areas having either cold winters and a semiarid climate (ecotype C) or cool winters and a sub-humid climate (ecotype D). In turn, the medium-high MSP group comprised ecotypes having temperate winters and a semiarid climate (ecotype E) or cool winters and a sub-humid climate (ecotype F).

3.2. Linear fixed-effects model

The standard fixed-effects analysis of variance for tree height showed highly significant ($p < 0.001$) trial, ecotype, population nested to ecotype, and ecotype by trial effects when using either CRU-based or WorldClim-based grouping information. There were almost threefold differences in height at age 15 among extreme trials. The trial having the highest height was Ovile, with a mean value of 11.31 ± 0.91 m (± SD), followed by Yatir West (8.70 ± 0.57 m). Conversely, the trial having the lowest height was Ademuz (4.01 ± 0.55 m), followed by Vedado de Zuera (4.47 ± 0.35 m). The remaining trials had mean height values varying between 5.5 m and 7.5 m.

The CRU-based classification of populations into ecotypes explained 23.4% and 52.9% of the total population and population by trial interaction effects with 6.2% and 21.5% of their degrees of freedom respectively (Suppl. Table S4). In comparison, the WorldClim-based classification explained only 8.5% and 26.7% of the population effect and the interaction between trial and populations (Suppl. Table S4). Thus, the CRU-based classification captured better the differential performance of ecotypes as depending on trial and was considered the classification of choice to summarise patterns of genotypic stability for the species. Assuming the CRU-based classification of populations, we found significant effects on survival ($p < 0.001$) of ecotype, population nested to ecotype and trial. However, the ecotype by trial interaction was non-significant ($p = 0.878$), suggesting stable ecotypic ranking across trials. Trials displayed contrasting survival rates. The trial having the highest survival was Altura (mean = 97.4 ± 7.1%), followed by Castglioncello (92.3 ± 3.4%), whereas the trial with the lowest survival was Yatir East (48.8 ± 14.2%), followed by Ovile (52.3 ± 17.8%). The remaining trials had survival rates varying between 67.8% and 84.1%.

3.3. Ecotypic stability

Model testing and selection for the ecotypic stability of tree height is presented in Table 2. Assuming homogeneity of residual variances across trials, the best fitting model based on the lowest AIC value was the AMMI–1 model; instead, BIC statistic favoured the simpler additive mixed-effects model. Nevertheless, all models allowing for heterogeneity of residual variances between trials provided a better fit (i.e., lower AIC and BIC) than their counterparts having homogeneous residuals. This outcome indicated that deviations of populations from ecotype means were heterogeneous across trials. The parameters of all five stability models assuming heterogeneity of residual variances are shown in Table 3. Among these, the Finlay–Wilkinson (F–W) model received ample support (i.e., showed both the lowest AIC and BIC). Based on F–W's model, the ecotype showing the largest sensitivity to improving growing conditions (i.e., the most plastic ecotype having phenotypes that change faster with the environment) was D ($\lambda_D = 2.420$, standard error (SE) = 0.611) followed by ecotype B

Table 2
Goodness-of-fit statistics of several stability models for tree height at age 15.

| Model | Homogeneous residual variance | | | Heterogeneous residual variance | | |
| | Nr parms[1] | Goodness-of-fit statistics[2] | | Nr parms[1] | Goodness-of-fit statistics[2] | |
		AIC	BIC		AIC	BIC
Additive	4	517.1	<u>526.7</u>	12	470.8	499.7
Shukla	9	514.6	533.9	17	473.1	509.2
Finlay–Wilkinson	8	516.6	535.8	**17**	**<u>460.1</u>**	**<u>498.6</u>**
AMMI–1	10	<u>515.8</u>	537.4	18	470.7	509.2
Eberhart–Russell	14	509.5	538.4	22	465.2	510.9

[1] Number of random parameters.
[2] AIC, Akaike's information criterion; BIC, Bayesian information criterion. All statistics is in smaller-is-better form; underlined values indicate preferred models according to either AIC or BIC criterion for either homogeneous or heterogeneous residual variance. Bold values indicate the model of choice.

($\lambda_A = 2.290$, SE = 0.591). Ecotype C had the lowest sensitivity ($\lambda_C = 1.986$, SE = 0.501) followed by ecotype A ($\lambda_B = 2.057$, SE = 0.520). The common residual variance σ_d^2 converged to 0, suggesting maximum residual stability. Heterogeneity in deviations of populations from ecotype means ranged from 0.012 (that is, almost no deviations) in Vedado de Zuera to 0.875 in Yatir East (Table 3).

Model testing for survival data indicated the superiority of an additive mixed-effects model over more complex stability models (results not shown), as ecotype by trial interaction effects were found irrelevant (i.e., σ_{ET}^2 being non-significantly different from zero). This suggested that ecotypic differences in survival were approximately constant across trials.

3.4. Mean comparison

Mean comparison of the ecotypes was carried out on the basis of the best fitting stability model (Table 4). For tree height, based on F–W's model with heterogeneous error, ecotype D was the best performer, followed by ecotypes F and E. Conversely, the ecotype having the lowest height was C. The absolute mean difference in tree height at age 15 between extreme ecotypes was 0.93 m (14.3% in relative terms). For survival, based on the additive mixed-effects model, the best surviving ecotype was F, followed by C and B. The ecotype showing the least survival was D, and the range of differences in mean survival between extreme ecotypes was 10.4% (14.2% in relative terms). There was a negative relationship between height and survival, being significant if ecotype F was not considered (Fig. 3a).

Overall, highly reactive ecotypes to improved growing conditions (e.g., those having a high λ_i such as ecotype D) tended to show the highest mean height, with low reactive ecotypes exhibiting the opposite pattern (e.g., ecotype C) (Fig. 3b). The only exception was ecotype B, which showed a relatively low height coupled with a relatively large λ_i. The combined information on the variability (according to λ_i values, Table 4) and the mean of tree height was used to compare a particular ecotype directly with others. Thus, the probabilities of a given ecotype outperforming other ecotypes were computed (Table 5). As a result, the ecotype showing larger probabilities was D (mean probability of 0.99 across comparisons; 100% frequency of having a probability > 50% of outperforming another ecotype), followed by F (mean value of 0.76, outperformed in more than 50% of all comparisons only by D). At the other extreme, ecotype C was consistently outperformed by all other ecotypes. Ecotype E showed an average performance, with consistently higher height than ecotypes A, B and C but lower height than D and F. These patterns were confirmed by the consistency of performance analysis carried out at country level (Suppl. Figure S3). Ecotype D showed consistent superiority in tree height regardless of the country of

Table 3
Restricted maximum likelihood (REML) estimates for different variance–covariance structures with heterogeneous (i.e., trial-specific) residual variance for tree height at age 15.

| Ecotype	Additive	Shukla	Finlay–Wilkinson		AMMI–1		Eberhart–Russell	
	σ^2_{ET}	$\sigma^2_{ET(i)}$	λ_i	σ^2_d	λ_i	σ^2_d	λ_i	$\sigma^2_{d(k)}$
A	0.012	0	2.057	0	0	0	2.054	0
B	0.012	0.041	2.290	0	−0.153	0	2.370	0.084
C	0.012	0.008	1.986	0	0.048	0	1.981	0
D	0.012	0.089	2.420	0	−0.389	0	2.415	0.001
E	0.012	0	2.259	0	−0.155	0	2.258	0
F	0.012	0.027	2.265	0	−0.253	0	2.237	0.011
Other variance components								
Population (ecotype)	0.125	0.135		0.122		0.130		0.121
Trial	4.763	4.646		–		4.397		–
Trial-specific residual variance								
Ademuz	0.169	0.171		0.177		0.180		0.172
Altura	0.226	0.223		0.225		0.227		0.214
Bet Dagan	0.461	0.479		0.437		0.442		0.453
Castel di Guido	0.560	0.537		0.544		0.529		0.558
Castiglioncello	0.874	0.756		0.832		0.865		0.790
Ovile	0.263	0.201		0.170		0.169		0.181
Vedado de Zuera	0.014	0.010		0.012		0.009		0.011
Yatir East	1.069	1.093		0.875		0.928		0.879
Yatir West	0.102	0.094		0.138		0.157		0.100

Table 4
Ecotype means based on a Finlay–Wilkinson model with heterogeneous residual variance (for height at age 15) and an additive mixed-effects model with homogeneous residual variance (for survival).

Ecotype	Mean height (m)	LSD[1]	Survival (%)[2]	LSD[1]
A	6.70	b c	77.1	a b c
B	6.74	b c	76.8	a b c
C	6.47	c	80.3	a b
D	7.40	a	72.7	c
E	6.89	b	75.8	b c
F	6.92	b	83.1	a

[1] LSD, Least Significant Difference. Different letters indicate significant differences between ecotype means ($p < 0.05$)

[2] Back-transformed values are shown, but the means comparison test is performed on angular-transformed data

Table 5
Probability of i-th ecotype outperforming the i'-th ecotype for height. Ecotype means and standard deviation (SD) for probability are also included.

	Ecotype i'							
Ecotype i	A	B	C	D	E	F	Mean	SD
A	–	0.43	1.00	0.03	0.17	0.15	0.36	0.39
B	0.57	–	1.82	0.00	0.00	0.00	0.28	0.39
C	0.00	0.18	–	0.02	0.06	0.05	0.06	0.07
D	0.97	1.00	0.98	–	1.00	1.00	0.99	0.01
E	0.83	1.00	0.94	0.00	–	0.00	0.55	0.51
F	0.85	1.00	0.95	0.00	1.00	–	0.76	0.43

4. Discussion

Until now, a joint analysis of extant data from different common-garden networks was absent in *P. halepensis* (Chambel et al., 2013), presumably limiting our understanding of the adaptive structure of this widespread conifer. In this work, we demonstrate the existence of relevant genotypic variation along with differences in phenotypic plasticity in tree height among ecotypes covering the whole distribution range of the species. Tree height can be considered a good proxy of aerial biomass for *P. halepensis* since height–diameter allometry

evaluation, while ecotype C was consistently inferior across the entire Mediterranean basin. Other ecotypes exhibited an inconsistent performance (i.e., a large GE interaction at country level): ecotype F was usually classified as inconsistently superior and ecotype A as inconsistently inferior. Finally, ecotype E showed an average performance across countries and ecotype B was the only ecotype showing a highly variable height performance which depended on the country.
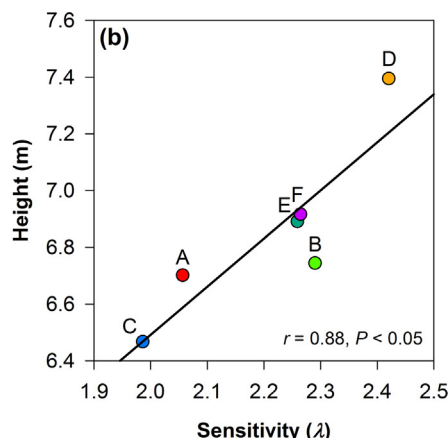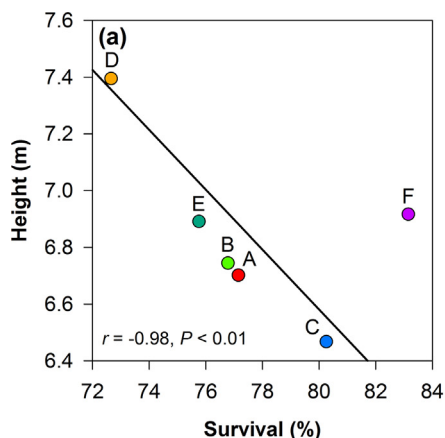
Fig. 3. Relationships at the ecotype level between (a) height and survival and (b) height and sensitivity to improved environmental conditions (Finlay–Wilkinson λ for height). The correlation in (a) does not include ecotype F, which represents the cool–wet edge of *P. halepensis* distribution and shows the highest survival across trials.

variation within this Mediterranean pine has proved to be absent (Vizcaíno-Palomar et al., 2016). In this way, we used height (and also survival) to disentangle the potential of *P. halepensis* populations to perform across a range-wide environmental gradient.

4.1. The significance of climate in revealing ecotypic patterns for growth

The assignment of populations to ecotypes based on climate information proved highly efficient in capturing genotypic and genotype-by-environment interaction effects for tree height, but only when using coarse climate records (CRU) as basis for classification. The relevance of climate in shaping adaptive patterns has been well recognized for *P. halepensis* (Calamassi et al., 2001; Climent et al., 2008; Schiller and Atzmon, 2009; Klein et al., 2013; Voltas et al., 2015, David-Schwartz et al., 2016). However, the suboptimal grouping derived from high-resolution data (WorldClim) was unexpected. In fact, the attribution of populations to ecotypes was similar across classifications, but the CRU-based grouping was geographically more consistent. Although inaccuracies in the geographic description of populations owing to diverse sources of trial information or even paucities of the meteorological stations cannot be discarded, we suggest that coarser spatial resolutions of climate data can account more faithfully for patterns of ecotypic differentiation in a wind-pollinated, widely distributed conifer such as *P. halepensis*. Abundant gene flow via efficient pollen dispersal, mediated by disturbances such as fire, is a key factor for genetic homogenisation and reduced kinship in *P. halepensis* (Shohami and Nathan, 2014). While this behaviour may limit adaptation at local scales, it could explain better the adaptive characteristics of large continuous populations as given by the spatial resolution of CRU records (about 2000 km^2 at mid latitudes).

Another important outcome is the striking similarities observed between our CRU-based climate classification of ecotypes and a recent definition of genetic groups based on molecular (SNP) information (Serra-Varela et al., 2017). The latter classification described seven different groups to which 49 populations of the species were ascribed, with at least three groups having a nearly perfect match with our grouping (corresponding to ecotypes C, D and F). Moreover, Serra-Varela et al. (2017) reported transition areas occupied by more than one genetic group simultaneously. In particular, populations from central and south Italy shared genetic pools of Greek and Tunisian populations, and southern Spain populations were genetically intermediate between central Spain and Moroccan population, which agrees well with our climatic classification. This realisation raises the question of whether the genetic classification using putatively neutral markers is providing clues on the molecular basis underlying adaptation of populations following the long-range colonization of the species. On one hand, some of the SNP markers used by Serra-Varela et al. (2017) may have been influenced by adaptive selection. However, the observed match between classifications is also supportive of the impact of selection processes under contrasting environmental conditions, which would have favoured different genotypes in populations subjected to distinctive bottlenecks during the post-glacial westward expansion process along the Mediterranean (Grivet et al., 2009).

4.2. What drives intra-specific variation in growth of Pinus halepensis?

A number of studies have postulated that variation for phenotypic plasticity in *P. halepensis* may be more important than standing genotypic variation in determining intra-specific changes for vegetative (Santos del Blanco et al., 2013; Vizcaíno-Palomar et al., 2016) and physiological traits (Baquedano et al., 2008). A central justification for this statement is the high genetic uniformity of the species for neutral markers (Soto et al., 2010). However, our results point to higher relevance of ecotypic differentiation in explaining phenotypic variability among populations for above-ground growth. The fact that previous studies on phenotypic plasticity for *P. halepensis* have been mainly

confined to a limited number of contrasting common-garden tests (≤ 3) could have tipped the balance towards a preponderance of plastic effects (e.g., Klein et al., 2013; Santos del Blanco et al., 2013). On the other hand, the range-wide conditions evaluated in our multi-environment trial represent a more reliable way to determine the magnitude of plastic effects vs. the importance of local adaptation. It should be noted that the variety of testing conditions matches well the array of site qualities in which *P. halepensis* can be found, which ranges from about 4 to 8 m of height at age 15 (site quality curves in Montero et al., 2001). Also, they include an optimal site for evaluating growth potential (Ovile, with mean tree height > 11 m). We reckon, however, that our methodological approach may often be limited to the analysis of a few traits (e.g., height, diameter) whose information is available (and can be faithfully compared) across different provenance trial networks.

In our analysis, the greatest support achieved by the F–W stability model indicates that ecotypic changes in plasticity can be described by different linear reaction norms to the mean phenotype across environments. It therefore suggests high predictability of ecotypic plastic responses in *P. halepensis* (see below), as opposed to alternative models which estimate stability as deviations from expected mean responses (e.g., Shukla) or as reactions to an unknown (underlying) environmental variable (e.g., AMMI–1). Despite significant ecotypic variation in plastic effects resulting from F–W λ's, the observed differences in mean height of *ca.* 15% among ecotypes dominated intra-specific growth patterns across trials. More specifically, the likelihood of a given ecotype outperforming another ecotype was far more related to standing ecotypic variation (r^2 of the linear regression of mean probability on mean ecotypic height = 0.90) than to differences in plasticity (r^2 of the linear regression of mean probability on F–W λ's = 0.66). This result indicates an important role for local (ecotypic) adaptation as triggered by climate for a species that can be found across very contrasting thermal and moisture conditions.

Although intra-specific patterns of tree growth were more dependent on mean ecotypic differences than on changes in plastic effects, ecotypic differentiation and plasticity (F–W λ's) followed the same direction in response to the productivity gradient of the network. This outcome can be interpreted as a signal of adaptive plasticity as proposed in evolutionary biology (Chevin et al., 2013). Whereas variation in ecotypic responses for vegetative traits were likely constrained under low-productive conditions, ecotypic differences were far more exposed in very favourable sites (e.g., outside the normal selective environments for this pine), perhaps unveiling hidden genetic variation (and, also, hidden reaction norms) (Schlichting, 2008). In regard of this, a number of studies indicate that specialization in favourable environments is linked to high plasticity, whereas the opposite is to be expected for specialization in harsh environments (Lortie and Aarssen, 1996; Valladares et al., 2007), as suggested for growth (Santos del Blanco et al., 2013) and photosynthetic traits (Baquedano et al., 2008) in *P. halepensis*. Particularly, specialization to harsh environments is usually associated with phenotypic stability and a conservative resource-use strategy (e.g., high water-use efficiency related to water conservation in *P. halepensis*; Voltas et al., 2008) as to avoid the construction of too expensive structures to be maintained under adverse conditions.

4.3. What drives intra-specific variation in survival of Pinus halepensis?

The likelihood of survival was variable at the ecotypic level and opposite to growth potential. As opposed yet to tree growth, the absence of ecotype-by-trial interaction suggests similar survival patterns across environments within the species. On the contrary, other studies on *P. halepensis* have reported variable survival of populations depending on testing conditions (e.g., Schiller and Atzmon (2009) and Taïbi et al. (2015) for survival at early stages). Our results, however, does not preclude the possibility that some populations may have shown significant interactions with the environment, although they

could not be statistically evaluated. Anyhow, our work points to the presence of a general adaptive syndrome by which less reactive ecotypes to ameliorated conditions (e.g., non-water-limited) would be associated with high survival rates and low growth, as proposed elsewhere (Valladares et al., 2007; Rueda et al., 2018). From an evolutionary perspective, the existence of trade-offs among traits (drought tolerance vs. growth) adds to the interactions between standing genetic variation and differential ecotypic plasticity in understanding fitness and forecasting responses to climate for *P. halepensis* (Franks et al., 2014). This issue definitely warrants a more detailed examination.

4.4. Geographical patterns of ecotypic differentiation

Geographical patterns of ecotypic variation have been reported for a number of anatomical, ecophysiological and morphometric traits in *P. halepensis* (Tognetti et al., 1997; Chambel et al., 2007; Climent et al., 2008; Voltas et al., 2008; Esteban et al., 2010; David-Schwartz et al., 2016), pointing to a well-structured assortment of adaptive responses following the postglacial long-range colonization of the western Mediterranean, after which genetic differentiation occurred (Gómez et al., 2005; Grivet et al., 2009). Mesic populations from the northern and eastern regions grow taller and allocate fewer resources to reproduction (Climent et al., 2008), are less water conservative (Voltas et al., 2008) and tend to exploit more shallow water than their drier counterparts from the southern and western regions (Voltas et al., 2015). This northeast–south-west cline was also found range-wide in our study, with ecotypes originating from sub-humid climates (D and F) showing higher growth than those found in semiarid and arid climates (A, B, C, and E) across most testing environments. In turn, the former ecotypes showed a high sensitivity to improved testing conditions (i.e., high plasticity), which confirms patterns already described at seedling stage (Chambel et al., 2007).

The performance above (high growth potential coupled with high sensitivity to improved conditions) is exemplified by ecotype D comprising mainly Greek populations, which thus exhibited general adaptation. Eastern populations from the Mediterranean basin bear a high genetic diversity and they likely encompass most functional variation of *P. halepensis* (Grivet et al., 2009). These populations outperform most other populations regarding aerial growth under the present climate envelope of the species. Therefore, they may perform at least as well as other populations under future conditions imposed by climate change, despite their slightly lower survival rates. Alternatively, populations from the driest ecological extreme (i.e., ecotypes A and B) showed specific adaptation to harsh environments, suggesting capacity to cope with climate change in exposed areas of the distribution of *P. halepensis* (i.e., those with high risk of habitat loss). Both types of material (generalists vs. specialists) may be useful to managers aimed at facilitating adaptive processes in the near future i.e., through deployment in reforestation activities (e.g., assisted migration) (Benito-Garzón and Fernández-Manjarrés, 2015) or by defining dynamic conservation units (Lefèvre et al., 2013).

5. Concluding remarks

The information derived from the range-wide coverage of our multi-environment trial network strengthens current knowledge on the structure of intra-specific variation of *P. halepensis*, which is based upon molecular data and functional traits, by broadening the scope of inferences to most conditions existing at present for this species. Local adaptation appeared more relevant than ecotypic variation in plasticity in explaining growth performance and survival patterns, reassuring the role of fast climate-driven selection following post-glacial Mediterranean recolonization. Typical adaptive profiles of generalists (i.e., sub-humid–cool climate populations from the eastern Mediterranean) vs. specialists (i.e., semiarid-cold climate populations

from the western Mediterranean) were identified and characterised among ecotypes. Altogether, our results build the foundations for tailoring intra-specific responses to climate and disentangling the relationship between adaptive variation and resilience towards climatic warming for a widespread Mediterranean conifer such as *P. halepensis*. This issue could be especially important at the rear edge of the species' distribution, where the greatest sensitivity is expected under warmer and drier conditions (Sarris et al., 2011; del Río et al., 2014; Benito-Garzón and Fernández-Manjarrés, 2015; Choury et al., 2017).

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2018.04.058.

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