The legacy of climate variability over the last century on populations' phenotypic variation in tree height

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Title

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1 **The legacy of climate variability over the last century on populations' phenotypic**

2 **variation in tree height**

3

4 **Running Title:** Phenotypic variation in tree height

5

6 **Abstract**

7 Phenotypic plasticity and local adaptation are the two main processes underlying trait

8 variability. Under rapid environmental change, phenotypic plasticity, if adaptive, could

9 increase the odds for organisms to persist. However, little is known on how environmental

10 variation has shaped plasticity across species ranges over time. Here, we assess whether the

11 portion of phenotypic variation of tree populations linked to the environment is related to the

12 inter-annual climate variability of the last century and how it varies among populations across

13 species ranges and age. To this aim, we used 372 647 individual tree height measurements of

14 three pine species found in low elevation forests in Europe: *Pinus nigra* Arnold, *P. pinaster*

15 Aiton and *P. pinea L.* Measurements were taken in a network of 38 common gardens

16 established in Europe and North Africa with 315 populations covering the distribution range

17 of the species. We fitted linear mixed-effect models of tree height as a function of age,

18 population, climate and competition effects. Models allowed us to estimate tree height

19 response curves at the population level and indexes of populations' phenotypic variation, as a

20 proxy of phenotypic plasticity, at 4, 8 and 16 years old, and relate these indexes to the inter-

21 annual climate variability of the last century. We found that phenotypic variation in tree

22 height was higher in young trees than in older ones. We also found that *P. pinea* showed the

23 highest phenotypic variation in tree height compared with *P. pinaster* and *P. nigra.* Finally,

24 phenotypic variation in tree height may be partly adaptive, and differently across species, as

25 climate variability during the last century at the origin of the populations explained between

1

26   51-69% of the current phenotypic variation of *P. nigra* and *P. pinea*, almost twice of the

27   levels of *P. pinaster.*

28

29   **Main conclusions:** Populations' phenotypic variation in tree height is largely explained by

30   the climate variability that the populations experienced during the last century, which we

31   attribute to the genetic diversity among populations.

32

33   **Keywords:** Black pine, Climate change, Developmental stage, Maritime pine, Mixed-effect

34   models, Stone pine.

1. Introduction

Climate change is reshuffling species distribution ranges from marine to terrestrial systems, altering current ecosystems functioning and structure through disruption of species interactions at temporal and/or spatial scales (Lenoir et al., 2008; Poloczanska et al., 2013). To survive under new climates, organisms can move to more favourable environments (Chen et al., 2011; Sunday et al., 2011), or persist *in-situ* by changes in their genetic composition or adjusting to environmental changes using phenotypic plasticity (Pulido and Berthold, 2004; West-Eberhard, 2003). Evolutionary responses to climate change will imply changes in allele frequencies that need one to many generations to arise (Bradshaw and Holzapfel, 2001; Franks et al., 2007; Reale et al., 2003). In contrast, plastic responses occur without changes in the genetic structure thus within one generation (Sultan, 2000; Valladares et al., 2014) and can sometimes be maintained across generations (Donelson *et al.*, (2018)). Therefore, phenotypic plasticity can provide a rapid response, whereas evolutionary responses need longer time depending on the generation length and number of offspring of organisms. For the particular case of trees, with very long generation times and large gene flow among populations, genetic adaptation occurs at long time scales (Savolainen et al., 2007). Although genetic adaptation can theoretically occur over just a few generations (Oddou-Muratorio and Davi, 2014), evolutionary adjustments to match new climates calculated using common garden data were estimated to be more than 1500 years for *Pinus sylvestris* (Rehfeldt et al., 2002). Therefore, plasticity is often the main mechanism for tree populations to respond *in-situ* to rapid climate change (Benito Garzón et al., 2019).

Environmental variation may promote differentiation in phenotypic plasticity among populations. Some studies have shown that more plastic genotypes are those promoted under greater variation (Lind & Johansson, 2007; Canale & Henry, 2010; Baythavong, 2011; Lázaro-Nogal *et al.*, 2015). However, phenotypic plasticity may not be always advantageous.

60   For example, high values of plasticity have been found to be associated with low values of

61   fitness-related traits such as survival, biomass or reproduction (e.g. Sánchez-Gómez *et al.*,

62   2006; Molina-Montenegro & Naya, 2012; Kreyling *et al.*, 2019). Likewise, changes in

63   plasticity can occur during the lifespan of organisms due to morphological and physiological

64   adjustments to the environment (Coleman et al., 1994; Evans, 1972; Mitchell and Bakker,

65   2014). For instance, Cornelissen *et al.*, (2003) showed trait variation with age in a survey

66   performed in 90 woody and semi-woody species, suggesting differences in phenotypic

67   plasticity with age. The pressure exerted by environmental cues is higher for seedlings than

68   for mature trees. For example, seedling root systems are located in the upper soil layers where

69   variation in soil moisture is greater than in the deep layers of the soil to which roots of mature

70   trees can get access. Consequently, we could expect greater plasticity in the early stages of

71   development that would allow them for coping with higher environmental variability. Taken

72   altogether, we could expect that phenotypic plasticity can vary across the species distribution

73   ranges and within-species lifespan.

74   Among-populations variation in tree traits attributed to local adaptation follows a

75   geographical pattern from the core to the margins across species ranges (Fréjaville et al.,

76   2020; Pedlar and McKenney, 2017). In the case of phenotypic plasticity, no clear

77   geographical patterns have been detected, although phenotypic plasticity variation among

78   populations is a very common feature for a wide range of species and traits (Benito Garzón et

79   al., 2019; Matesanz and Ramírez-Valiente, 2019), and environmental variability could have

80   promoted differences in plasticity (Sultan and Spencer, 2002).

81   Strictly speaking, phenotypic plasticity should be measured on individual genotypes

82   (Pigliucci et al., 2006). Relaxing this strict definition and focusing on populations across

83   species ranges, phenotypic plasticity can be addressed in relation with the ecology of the

84   species (Gianoli and Valladares, 2012; Richards et al., 2006). A relatively abundant source of

85   phenotypic data covering species ranges comes from common gardens. Ideally, common

86   gardens should be a minimum of three to capture non-linear trends (Arnold *et al.*, 2019) and

87   installed across large environmental gradients in which a suite of populations from varied

88   origins are planted. With these experimental designs, estimating populations' phenotypic trait

89   variation, as a proxy of phenotypic plasticity at population level, is straightforward using

90   standardised indexes of phenotypic response curves (Arnold *et al.*, 2019, Valladares *et al.*,

91   2006).

92   *Pinus nigra* Arnold, *P. pinaster* Aiton and *P. pinea L* are distributed across the

93   Mediterranean basin sharing common features: they are phylogenetically related species with

94   a common ancestor (Klaus and Ehrendorfer, 1989); they present patchy distributions with

95   differentiated patterns of genetic diversity and local adaptation resulting from the particular

96   orography, climate and recent history of species' expansions from refugia in the

97   Mediterranean basin (Fady, 2012; Médail and Diadema, 2009); and they are threatened by

98   climate warming in their current habitat, as they are present in low elevation forests across

99   most of their range. Hence, we expect to find common biological strategies, including

100   phenotypic plasticity. Although we also expect differences because the habitat of *P. pinea*, the

101   most thermophilic of these three pines, was extremely reduced during the ice ages but not that

102   of the other two pines which could migrate down along mountain slopes during the cold

103   periods of the Pleistocene (Vendramin et al., 2008). Then, we expect that *P. pinea* success

104   may rely more on phenotype variation linked to the environment than to local adaptation as in

105   the case of the other two pines.

106   Here we used tree height, a fitness-related trait (King, 1990; Savolainen et al., 2007),

107   measured in a wide network of common gardens established in Europe and North Africa for

108   *P. nigra*, *P. pinaster* and *P. pinea* (Vizcaíno-Palomar et al., 2019). We fitted linear mixed-

109   effect models of tree height to: 1) calculate tree height variation response curves at the

population level for the three species; 2) estimate populations' phenotypic variation (as a proxy of populations' phenotypic plasticity) in tree height across species ranges and with tree age; and 3) assess whether this phenotypic variation in tree height of the populations is related to the inter-annual climate variation of the last century and thus, appears to be adaptive.

2. Material and methods

116 **2.1. Common gardens, species and phenotypic data**

117 We used tree height recorded in common gardens (which we also call trials) for three pine

118 species: *P. nigra* Arn., *P. pinaster* Aiton and *P. pinea* L. (Fig. A1). For *P. nigra*, we used 192

119 222 measurements of individual tree height recorded in 15 trials distributed across three

120 countries (France, Germany and Spain) planted with 78 populations from geographic origins

121 (provenances) covering the range of the species. Trials were planted between 1968 and 2009

122 and tree heights were measured over a period of 16 years. For *P. pinaster*, we used 123 801

123 measurements of individual tree height recorded in 14 trials established across three countries

124 (France, Morocco and Spain) and 182 provenances covering the range of the species. Trials

125 were installed between 1966 and 1992 and tree heights were measured over a period of 32

126 years. For *P. pinea,* we used 56 624 measurements of individual tree height recorded in 9

127 trials established in France and Spain, where a total 55 provenances covering the range of the

128 species were planted. Trials were established between 1993 and 1997, and tree heights were

129 measured over a period of 20 years. These databases gather alive trees, thus if selective

130 filtering have occurred like differential survival across populations, trials and age is not

131 accounted. Further description of these databases can be found in Vizcaíno-Palomar *et al.*

132 (2019), and all phenotypic data used in this study are available on the open-access repository

133 of Zenodo (Vizcaíno-Palomar et al., 2018a, 2018b, 2018c) for *P. nigra*, *P. pinaster* and *P.*

134 *pinea*, respectively.

135   To analyse the effect of age on tree height variation, we defined three classes of age at

136 4, 8 and 16 years after trees were planted in the trials. We selected the same ages for the three

137 species to facilitate comparisons, while the three different ages aimed at capturing different

138 life stages, like seedling, juvenile and young adult, within the lifespan of tree individuals.

139

2.2 Competition effects among trees in the common gardens

For each planted tree in each trial (hereinafter 'focal tree'), we computed a competition index to account for the neighbourhood effects coming from the four closest trees situated at the cardinal directions of North, East, South and West of the focal tree. Specifically, for each focal tree, we summed the number of trees taller than the focal tree, thus this index ranges between 0 and 4. For the cases where this information was absent (*P. nigra* in the French trials of Levens and Verdun and in German trials; and for *P. pinaster* in French and Morocco trials), we approached the competition index by fitting a generalized linear-mixed effect model as a function of tree height and age (Appendix A for further information).

2.3. Climate data

We used the EuMedClim dataset that provides annual measurements between 1901 and 2014, at 30 arc-seconds (~ 1km) of resolution (https://gentree.data.inra.fr/climate/datasets/; Fréjaville & Benito Garzón, (2018)). We used 21 climatic variables related with either annual or seasonal precipitation and temperature related variables (Table A1). From this database, we computed the following climate-related variables and indices:

i) Long-term climate effect on trees' height population ($clim_p$) is the average climate at the population origin between the beginning of the 20th century (1901) and the year before the trees were planted in the trials. This long-term climate reflects the average climate that occurred when the planted seeds were generated, and hence it could be related to genetics.

ii) Short-term climate effect on trees' height population ($clim_t$) is the average climate at the trial of the last 3 years. This short-term climate effect was defined to reflect tree height variation response as a proxy of phenotypic plasticity to recent climate.

iii) Inter-annual climate variation indices of seven climate variables related to temperature and precipitation during the 20th century at the population origin. We computed

165   the coefficient of variation (cv = standard deviation/mean) to reflect the past average climate

166   variation encountered by the tree populations at their location origin from 1901 until the trees

167   were planted. Specifically, we computed the coefficient of variation (cv) of the mean annual

168   temperature (cv bio1), cv of the mean diurnal temperature range (cv bio2), cv of the

169   maximum temperature of the warmest month (cv bio5), cv of the minimum temperature of the

170   coldest month (cv bio6), cv of the annual precipitation (cv bio12), cv of the precipitation of

171   the wettest month (cv bio13) and cv of the precipitation of the driest month (cv bio14). We

172   calculated the coefficient of variation of temperature-related variables in degrees Kelvin. For

173   precipitation-related variables, we summed 1 to the precipitation values to avoid mean values

174   between zero and one that would provide meaningless cv values. We standardized all climate-

175   related variables and indices for further analyses.

176

177   **2.4. Statistical analyses**

178   We used linear mixed-effect models to fit tree height accounting for tree age, genetics

179   (approached by the climate at the population origin, $clim_p$), plasticity (approached by the

180   climate at the trial, $clim_t$) and competition among trees (approached by the competition

181   index). Based on the fitted models, we computed tree height response curves at the population

182   level across the climatic range covered by the trials at age 4, 8 and 16 to compute populations'

183   sensitivity to climate (as a proxy of populations' tree height plasticity).

184

185   **2.4.1. Tree height response curves at the population level**

186   For each species, we selected one climate variable for the population ($clim_p$) and another for

187   the trial ($clim_t$). We selected those climate variables that were highly correlated with tree

188   height (the response variable) and represented well the climate variation gathered in the

189   network of common gardens. To do this, we used two complementary analyses: 1) linear

190   mixed-effects models and 2) principal component analyses (PCA) of the climate variables (for

191   further description in Appendix B). For *P. nigra,* we selected mean annual temperature (bio1)

192   for $clim_t$ and annual water availability (WAI) for $clim_p$. For *P. pinaster,* annual potential

193   evapotranspiration (PET) for $clim_t$ and winter precipitation (prec.djf) for $clim_p$. And for *P.*

194   *pinea,* maximum temperature of the warmest month (bio5) for $clim_t$ and summer precipitation

195   (prec.jja) for $clim_p$ (see Appendix C, Table A2 and Fig. A2).

196   We fitted linear mixed-effect models of tree height accounting for tree age, $clim_p$,

197    $clim_t$ and competition. The model equation takes the form (Eq. 1):

198    $H = \sum_{i=1}^{p} \alpha_i X_i + \varepsilon_{ran} + \varepsilon_{res}$ Eq. 1

199   where *H* is tree height, α_i is the set of *p* parameters associated with the main and interactive

200   fixed effects of X_i (tree age, $clim_p$, $clim_t$, competition), ε_{ran} is the variance component

201   associated with the random terms, and ε_{res} is the residual distributed error following a

202   Gaussian distribution (but see the Results section for the case of *P. nigra*).

203   The saturated model for the fixed part, $\sum_{i=1}^{p} \alpha_i X_i$, contained the linear and quadratic

204   terms for each explanatory variable and all the potential pair-wise, three and four variable

205   interactions (i.e. age × $clim_p$, age × $clim_t$, $clim_p$ × $clim_t$, age×competition, age × $clim_p$ × $clim_t$,

206   and age × $clim_p$ × $clim_t$ × competition). The random part of the model allowed us to consider

207   the hierarchical nature of the data derived from the experimental design (populations nested

208   within blocks, and blocks nested within trials, as populations are not fully crossed in trials,

209   Vizcaíno-Palomar et al. (2019)); the temporal autocorrelation for individual trees measured

210   over years; and the residual sources of variation not included in the fixed effects (such as soil,

211   variation occurring at smaller spatial scales than blocks, etc.).

212   We selected the best-supported model starting from a saturated model following a

213   hierarchical backward selection procedure (Burnham and Anderson, 2002; Zuur et al., 2009),

214   following six steps (see Appendix D for further information). The variance explained by the

215　model was assessed by pseudo-R^2 (Nakagawa and Schielzeth, 2013) and by the capacity of

216　generalization of the model (CG), that is to calculate the Pearson correlation coefficient, r,

217　between a model fitted with the 2/3 parts of the data and independently validated with the

218　remaining 1/3 part of the data. We controlled collinearity between explanatory variables in the

219　best-supported model using the variance inflation factor (VIFs) settled to maximum value of 5

220　which is considered acceptable (Belsley, 1991). All analyses were done with the R version

221　3.6.1 (R Core Team, 2019) run in linux-gnu operating system .

222　　　Using the best-supported model for each species, we predicted tree height response

223　curves at the population level for each population across the climatic range covered by the

224　trials, $clim_t$, at 4, 8 and 16 years. Specifically, we fixed the competition index to a null effect,

225　and predicted tree height response curves at the population level for a given tree age and

226　climate at the population origin ($clim_p$) along the climate of the trial ($clim_t$) varying between

227　the 99% percentiles observed in $clim_t$ data.

228

229　**2.4.2. Population's phenotypic plasticity in tree height**

230　Although phenotypic plasticity is generally addressed at the genotype level, this requirement

231　can be relaxed in range-wide approaches with a marked interest at the population level

232　(Gianoli and Valladares, 2012; Richards et al., 2006). Accordingly, we used tree height

233　response curves at the population level at 4, 8 and 16 years to estimate the part of the tree

234　height that is mostly attributed to the phenotypic plasticity of each population (reviewed in

235　Valladares *et al.*, (2006)).

236　　　1) Phenotypic plasticity index (PP) was computed as follows:

237　$PP = (H_M - H_m)/H_M$　　　　　Eq. 2

238　where H_M is the highest phenotypic value (height) predicted across the tree height response at

239　the population level and across the climatic range studied. H_m is the lowest phenotypic value

240   predicted across the climatic range studied. In PP, phenotypic plasticity increases from zero

241   (null plasticity) to one (maximum plasticity).

242   2) Coefficient of variation of the phenotypic response (CV) was computed as follows:

243   CV = sd(H)/mean (H)   Eq. 3

244   where H is the predicted phenotypic value (height) at each value of the climatic range covered

245   across the climate at the trials, and sd is the standard deviation. This index reflects the range

246   of phenotype variation across the studied range. In CV, phenotypic plasticity is null if the

247   index is equal to zero. Higher values of CV represent higher plasticity without upper bound

248   values.

249   We tested for phenotypic plasticity differences among and within species and classes

250   of age with independent analyses of the variance of the PP and CV indexes. If there was

251   heterogeneity in the variance across levels, we performed analyses of the variance type II

252   (Welch test). We computed post-hoc pairwise comparisons of Tukey HSD (Honestly

253   Significant Difference), or Games-Howell test if heterogeneity in the variance, or the Kruskal

254   Wallis test if normality assumptions were not met.

255   We computed Spearman's rank-order correlation coefficient, ρ, between the

256   phenotypic plasticity of the populations and the latitude and longitude at each population

257   origin to assess whether populations' phenotypic plasticity follow any general geographical

258   pattern. These populations' phenotypic plasticity indexes and ρ coefficients are then

259   represented across species ranges.

260

261   **2.4.3. The effect of the inter-annual climate variability during the 20th century on**

262   **populations' phenotypic plasticity in tree height**

263   For each species and class of age, we tested whether inter-annual variation of climate at the

264   population origin during the last century explains the current levels of tree height mostly

265   attributable to phenotypic plasticity calculated with the two indices (PP and CV). To this end,

266   we fitted linear fixed-effect models between the populations' phenotypic plasticity as a

267   function of the selected group of climate variables (see Inter-annual climate variation indices

268   in Climate data section) (Eq. 4).

269    $PI_j = \sum_{i=1}^{p} \alpha_i X_i + \varepsilon_{res}$ Eq. 4

270   where PI_j is the phenotypic plasticity of a population calculated either using the PP or CV

271   index at tree age j (j= 4, 8 or 16 years), α_i is the set of p parameters associated with the effects

272   of X_i (cv bio$_i$) and ε_{res} is the residual error. Models were fitted with a Gaussian distribution of

273   errors and identity link function. An automatized backward selection procedure was used to

274   choose the best-supported model (stepAIC function in MASS package, Venables & Ripley,

275   (2002)). We settled VIF settled to 5 to detect collinearity. Appropriateness of the models was

276   assessed by plotting residuals vs. fitted values, qq-plots and the Cook's distance that identify

277   outliers in the data that could over-influence the model fitting, and if necessary, they were

278   removed from the analysis.

3. Results

3.1. Tree height response curves at the population level

Overall, tree age made the largest contribution to explain tree height variation , followed by competition effects, climate at the trial ($clim_t$) and climate at the population origin ($clim_p$) in *P. nigra* and *P. pinea*, whereas climate at the trial contributed more than competition in *P. pinaster* (Table 1; see ΔAIC comparisons). The mean annual temperature at the trial had a positive effect on tree height variation in *P. nigra* (Fig.1a), but in the other two species, above a threshold of evaporative demand (either expressed in mm by annual potential evapotranspiration or degrees Celsius by the maximum temperature of the warmest month), the temperature had a negative effect (Fig.1 e),i)). The contribution of the interaction term $clim_t \times clim_p$, that is tree height variation among populations, was significant in *P. nigra* and *P. pinaster*, while it was negligible in *P. pinea* (Table 1 and Fig.1 a),e),i)). See Appendix E for further details about the linear mixed-effect models.

3.2. Population's phenotypic plasticity in tree height

The portion of tree height variation attributable to phenotypic plasticity decreased significantly with age in the three species, i.e. young trees were the most plastic ones (Fig. 2, Tables A4 and A5). The highest values of phenotypic plasticity in tree height were found in *P. pinea* and the lowest in *P. nigra* for the two indices analysed (Fig. 2).

Geographical patterns of phenotypic plasticity across species ranges were found in *P. pinea*, with high Spearman's ρ values between latitude and phenotypic plasticity in PP and CV indices (Fig. 1, Fig. A4). Specifically, phenotypic plasticity values at 4 years were positively correlated with latitude (for PP and CV indices, ρ = 0.91), while from 8 years onwards, they were negatively correlated (for PP and CV indices, ρ = -0.90 at 8 and 16 years, and for PP and CV indices, ρ = -0.91 at 8 and 16 years). Similar though weak patterns with latitude were

14

304   found in *P. nigra* and curvilinear trends across ages with longitude (Fig. A5). For *P. pinaster*,

305   we did not find any geographical (Fig. A5).

306

3.3. The effect of the inter-annual climate variability during the 20th century on

307

308   **populations' phenotypic plasticity in tree height**

309   Overall, climate variability at the population origin during the last century explained larger

310   levels of the portion of tree height variation attributable to phenotypic plasticity among

311   populations in *P. nigra* (explained variance ranged between 0.51 and 0.52) and *P. pinea*

312   (between 0.59 and 0.69) than in *P. pinaster* (between 0.27 and 0.29). In addition, we found

313   more homogeneous patterns of phenotypic plasticity within species than among species

314   (Table 3).

315   Among species, we found the coefficient of variation, cv, of the mean annual

316   temperature and the cv of annual precipitation as common predictors across ages for the three

317   species with some exceptions in *P. pinea* (Table 3). However, their effects on the plasticity of

318   the populations changed with age and the species. For instance, in *P. nigra* and *P. pinea*: the

319   effects of the cv of mean annual temperature and precipitation were negative on phenotypic

320   plasticity at 4 years, while at 8 and 16 years these effects were positive. On the contrary, the

321   cv of the mean annual temperature and cv of annual precipitation had negative effects across

322   ages in *P. pinaster*.

323   Within species, we found consistent patterns of the climate variability effects on

324   plasticity across ages, with some exceptions in *P. nigra* and *P. pinea*. For these two species,

325   we found that the cv of extreme temperature variables, e.g. maximum temperature of the

326   warmest month, had positive effects on plasticity levels at 4 years, but negative at 8 and 16

327   years (Table 3). On the contrary, the cv of climatic related variables representative of average

328   climates, e.g. annual mean temperature, had negative effects on plasticity at 4 years but the

329   opposite at 8 and 16 years. In *P. pinaster*, climate variability had consistent negative effects

330   on plasticity across ages, except the cv of the precipitation of the wettest month that was

331   positive (Table 3). Finally, we removed from our analyses the Artvin population (Turkey) of

332   *P. pinea* at 4 and 8 years according to the Cook's distance criterion without significant impact

333   on the final parameter estimates.

334   For illustrative purposes, we plotted populations' phenotypic plasticity calculated with

335   PP and CV indices along the coefficient of variation, cv, of the climatic variable that had the

336   highest size effect in absolute terms in each fitted model. Generally, among species, either in

337   PP or CV, did not share the same climate variable driving the largest effect on populations'

338   phenotypic plasticity, but within species, they did (Fig. 3 and Fig. A6). Within species, the

339   effects of the climate variable varied with age, from negative to positive, except in *P. pinaster*

340   where the negative effect remained invariable with age (Fig. 3 and Fig. A6).

4. Discussion

The use of range-wide multi-year tree height measurements compiled from common gardens and linear mixed effect models allowed us to quantify the effect of age, population, climate and competition across the distribution ranges of three Mediterranean pines. We use phenotypic variation at population level as a proxy of population phenotypic plasticity and show that: 1) tree height phenotypic plasticity was higher in young trees than in older ones; 2) *P. pinea* showed the highest phenotypic plasticity values in tree height, followed by *P. pinaster* and *P. nigra;* and 3) the climate variability during the last century at the population origin (i.e. the genetic diversity among populations) explained between 51-69% of the current phenotypic plasticity of *P. nigra* and *P. pinea*, almost twice of the levels of *P. pinaster*.

4.1. Tree height response curves at the population level

Tree height response curves at the population level were mainly driven by temperature-related variables (mean annual temperature, annual potential evapotranspiration and maximum temperature of the warmest month), and in general, rising temperatures led to higher trees up to a certain value (Fig. 1). This result is in agreement with previous studies suggesting that higher heights in pines are found at warmer sites, if drought is not limiting (Lines et al., 2012; Vizcaíno-Palomar et al., 2016). This could be explained because warm temperatures, up to a certain threshold, increase photosynthetic capacity, resulting in a higher rate of carbon assimilation (Reich and Oleksyn, 2008; Way and Oren, 2010). Beyond this threshold, it can imply the opposite effect. Accordingly, in *P. pinaster* and *P. pinea* tree height decreases when the evaporative demand is too high due to stomatal closure and reduction of the photosynthetic activity (Mazza et al., 2014; Pasho et al., 2012). However, we did not find that threshold in *P. nigra.* This could be explained because *P. nigra* does not reach its maximum tree height within the range of climate covered by the sampled trials, which covers mostly

cool temperatures as it is shown in Fig. A1. Moreover, tree height population variation, as a proxy of phenotypic plasticity, can be promoted by other factors either biotic or abiotic, apart from the climate that we considered. For example in *P. pinea*, Mutke *et al.*, (2010, 2013) showed microsite effects apparently related with soil variation either in texture or pH that could have also contributed to the phenotypic variation found in the species. In addition, biotic drivers such as intraspecific competition, herbivory, etc. can contribute to phenotype variation as well.

The main climatic drivers in tree height variation among populations were precipitation (in *P. pinaster* and *P. pinea*) and annual water availability (in *P. nigra*) (Fig. 1). This points out to the selective role of water availability across the range of these mostly Mediterranean species (Pigott and Pigott, 1993; Siepielski et al., 2017). Our findings may suggest that evolutionary processes leading to local adaptation (i.e. population differentiation) in tree height were partly driven by water availability (Aranda et al., 2010; Pardos and Calama, 2018), although temperature-related variables have been also reported to drive local adaptation in tree height in these pine species (Fréjaville et al., 2020). The highest variation in tree height among populations was found for *P. nigra* and *P. pinaster* (Fig. 1 a) e)). This intraspecific variation could be the result of adaptations to the local climate. For example, *P. pinaster* populations from the south of the distribution are better adapted to drought as they invest higher biomass to root and less to stem development than populations from northern parts of the distribution (Aranda et al., 2010). In *P. nigra*, differences among populations in tree growth, height allometry among others have also been reported (Thiel *et al.*, 2012, Vizcaino-Palomar et al. 2016). Contrarily, *P. pinea* showed negligible variation in tree height among populations (Fig. 1i)). This result is in agreement with previous studies reporting either little genetic variation in morphological and physiological quantitative traits, e.g.

390 photosynthesis, biomass partitioning, specific leaf area, etc. (Court-Picon et al., 2004; Mutke

391 et al., 2010; Pardos and Calama, 2018) or even null variation (Chambel *et al.*, 2007).

392

393 **4.2. Population's phenotypic plasticity in tree height**

394 Although we found that the three pine species present moderate-high capacities to respond to

395 changes in the environment by plastic adjustments in tree height, *P. pinea* stood out for being

396 the most plastic (Fig. 2). *P. nigra* and *P. pinaster* have moderate-high neutral genetic diversity

397 and differentiation in quantitative traits (Soto et al., 2010), while *P. pinea* almost lacks any of

398 it. This latter could suggest that this species may have undergone selection for increased

399 plasticity instead of differentiation among populations. Low levels of genetic diversity are

400 compatible with high levels of epigenetics (heritable phenotype changes that do not entail

401 alterations in the DNA sequence), as it has been shown in *P. pinea* by Sáez-Laguna *et al.*,

402 (2014), with a potential link with phenotypic plasticity. However, this link is to date unclear,

403 different studies have also stated that high genetic diversity can favour phenotypic plasticity

404 as it increases the chances of possessing advantageous alleles (see for example, Doi *et al.*,

405 (2010); Harter *et al.*, (2015)), but also the opposite trend has been shown (Castillo et al., 2018;

406 Kreyling et al., 2019).

407   We found that pine seedlings presented higher abilities to respond to changes in

408 climate, i.e. to respond plastically, than young adult trees (Fig. 2). This result indicates that

409 the capacity to respond plastically varies along the lifespan of tree individuals. The first stages

410 of recruitment are critical for plant establishment, and hence greater capacity to respond

411 rapidly to changes in the environment can be advantageous. For instance, plasticity in tree

412 height can be crucial to avoid competition by reaching light and hence survive. In addition,

413 small changes in the environment can be more noticeable for seedlings than to saplings or

414 adult trees. For instance, soil moisture variation is higher in the shallow layers of the soil than

415   in deeper ones, and maybe this has selected for greater phenotypic plasticity in tree height at

416   the early stages of development. As an explanation of the underlying mechanism governing

417   this pattern in phenotypic plasticity, we could suggest that the higher pressure of

418   environmental cues at the seedling stage may promote more gene expression for plasticity

419   than at later stages if tree height plasticity is genetically controlled and by the same group of

420   genes (for example this happens in tree height in *P. pinaster*, Miguel et al., (2020)), although

421   this need further research to be tested. But also, plantation effects which can vary depending

422   on the site, the planting team and the planting date could have inhibited the expression of

423   plasticity found. Altogether, the existence of phenotypic plasticity variation across ages

424   suggests that plasticity in tree height is a dynamic trait along the lifespan of tree individuals.

425   PP and CV indices provided similar results, i.e. ranked species and classes of age

426   identically, but differed in the order of magnitude, i.e. we got higher values in the PP index

427   than in the CV one (Fig. 2). We recommend the use of standardised indices with bounded

428   limits (like the PP index) as they are useful to interpret whether the given levels are high or

429   low. Finally, our phenotypic plasticity values are comparable in terms of magnitude across

430   species because they represent the highest phenotypic plasticity displayed by a given species,

431   despite these values are tightly linked to the climate variable of the trial used to fit the model

432   for each species.

433

434   **4.3. The effect of the inter-annual climate variability during the 20th century on**

435   **populations' phenotypic plasticity in tree height**

436   Our findings where a sizeable portion of tree height variation attributable to phenotypic

437   plasticity is explained by climate variation at the population origin during the 20th century

438   suggest that a part of tree height plasticity is adaptive and results from natural selection to

439   climate variability (Table 3). This result was consistent for the three Mediterranean species;

but past climate variability had a greater impact on the current levels of phenotypic plasticity in *P. nigra* and *P. pinea* than in *P. pinaster*.

Our expectation was that those populations subjected to greater variability in climate during the last century would display greater plasticity in tree height. This was true at early stages of development in *P. pinea* and in older trees in *P. nigra* as we found that those populations exposed to greater variation tended to be more plastic in tree height (Fig. 3). Previous studies have also reported similar results where phenotypic plasticity increases in response to more variable environments over time, for example in *Convolvulus chilensis* and *Senna candolleana* (Gianoli and González-Teuber, 2005; Lázaro-Nogal et al., 2015). However, this was not the general rule as we also found the opposite trend: at early stages in *P. nigra,* across ages in *P. pinaster,* and from 8 years onwards in *P. pinea.* These findings suggest that climatic cues promoting plastic responses in tree height may change across the lifespan of tree individuals and that they are species-dependent.

Because past climate variability had partially driven phenotypic plasticity in tree height, we expected to find geographical patterns arising among populations for phenotypic plasticity. Nonetheless, we only identified latitudinal patterns for *P. pinea* varying with age; while for the other species, unclear or no geographical patterns were found (Fig. 1 and Fig. A5). We expect that in *P. nigra* and *P. pinaster* other factors (e.g. species' demography, gene flow, etc.) together with climate, could be playing roles that are more fundamental in promoting plasticity. Taken altogether, non-uniform phenotypic plasticity across species ranges is ubiquitous in nature (Matesanz and Ramírez-Valiente, 2019), and our results point out that many factors may promote plasticity variation.

4.4. Implications of phenotypic plasticity for evolutionary responses to climate change

464   Among the three studied species, *P. pinaster* combines high values of plasticity in tree height

465   with high differentiation among populations (Fig. 2), suggesting good chances to respond to

466   climate change in the short-term through phenotypic plasticity, if adaptive, and keeping

467   evolutionary potential to get adapted in the long-term to the new environment (Pigliucci,

468   2005; Richards et al., 2006). *P. pinea* presents the highest phenotypic plasticity out of the

469   three studied species, but combined with low differentiation among populations and low

470   genetic diversity (Fig. 2), which makes plasticity virtually the unique way for this species to

471   respond to changes in the environment. However, we cannot rule out the existence of trade-

472   offs among traits. For example, in root growth dynamics *P. pinea* was less plastic than *P.*

473   *pinaster* and P. *nigra* (Toca *et al.*, 2019) but intraspecific variation was neglected.

474

475   **4.5. Limitations**

476   Our findings represent well the expected phenotypic plasticity of the populations in tree

477   height in planted forests associated to these climatic gradients. In natural populations, natural

478   regeneration and recruitment, competition among individuals within and among species,

479   biotic and community level interactions, etc., could significant affect tree height variation and

480   hence phenotypic plasticity (Ruiz-Benito et al., 2012). Tree height sensitivity to drought,

481   disturbances, as fires and other climate change related variables have not been directly

482   addressed in our analysis, limiting our understanding of the future of the natural populations

483   that will be threatened by global changes. In addition, our models are limited to the climatic

484   gradients covered by the network of common gardens we analysed. For example, we could

485   have underestimated phenotypic plasticity in *P. nigra* because the maximum tree height is not

486   reached within the mean annual temperature range studied. Also, our models, and hence the

487   estimates of phenotypic plasticity, are representative of the genetic pool after the selective

488   filtering that could have occurred within populations. For example, differences in survival are

489 reported for some of the trials that we used for *P. pinaster* (Benito Garzón *et al.*, 2011), but no

490 differences have been reported for *P. pinea* (Mutke *et al.*, (2010, 2013)). An additional

491 limitation comes from the different ontogenetic stages that the different species can have at 4

492 years. For example, there is a trial in *P. pinea* where ontogeny is delayed in comparison to the

493 rest of the trials (Mutke et al., 2010). Other environmental and biological drivers such as

494 demographic history and micro-environmental differences in the experimental set-ups that can

495 drive tree height variation are only considered in the random part of our models.

496 Complementary approaches as those coming from dendrochronology and genomics can fill

497 the gap to better understand the future of tree growth under climate change.

498

499 **4.6. Conclusions**

500 Our findings highlight that tree height is a plastic trait and varies across species, even

501 phylogenetically related ones. Moreover, part of this plasticity appears to be adaptive, or at

502 least differentiated, which indicates adaptation via natural selection. Also, plasticity for tree

503 height decreases with increasing age, indicating that it may become a less important trait with

504 age. Within species, there is no trend of increasing or decreasing plasticity with latitude,

505 indicating that predictions based on geography will be hard to make. *P. pinea* has

506 significantly more plasticity than other pines, indicating that it could be a compensatory

507 mechanism for lack of diversity to get adapted.

508

23

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768

Tables

Table 1. Selection of the random and fixed effects of the tree height models in response to

age, $clim_t$, $clim_p$ and competition index using the Akaike Information Criterion (AIC) for the

three pine species.

Table 2. Detailed description of the best-supported model for each pine species analysed

including the family distribution and link function, the variance and standard deviation for the

random effects (Var and SD respectively); and the estimated parameter and standard error for

the fixed-effects (Estimate and SE, respectively).

Table 3. Results of the linear fixed-effect models between phenotypic plasticity indexes (P.I.)

and the coefficient of variation of the climate variables (cv bio#). One sub-table is included

for each pine species, a), b) and c). Each sub-Table shows the results for the two indices and

the three classes of age analysed. 4 years: green, 8 years: orange and 16 years: blue.

Figures

Figure 1. Tree height response curves at the population level across $clim_t$ particularized for

three different origins of populations (High, Average and Low in terms of $clim_p$ values) and

for the three classes of age (4 years: green, 8 years: orange and 16 years: blue) for (a) *P.*

nigra, (e) *P. pinaster* and (i) *P. pinea*. Populations' phenotypic plasticity values (PP index) for

the three classes of age across the species natural distribution ranges are plotted in the maps. 4

years: (b), (f) and (j), 8 years: (c), (g) and (k); and 16 years: (d), (h) and (i). Geographical

patterns: Purple continuous lines indicate a high Spearman ρ coefficient, and discontinuous

lines mean low values. Arrows indicate the increasing direction of phenotypic plasticity.

Brown discontinuous lines indicate a curvilinear trend. Maps are plotted using the Lambert

azimuthal equal-area projection.

Figure 2. Phenotypic plasticity values of the PP index, left side, and CV index, right side, for

the three species and for the three classes of age (4 years: green, 8 years: orange and 16 years:

blue). Capital letters denote statistically significant differences among species, while lower

case letters denote differences across classes of age within species.

Figure 3. Tree height variation prediction attributable to phenotypic plasticity (black dotted

lines) across the coefficient of variation, cv, of the climatic variable with the highest size

effect in absolute terms and populations' phenotypic plasticity calculated with the PP index

800   (dot colours) for the three classes of age and pines species. Legend: Dot colours represent the

801   country of origin of the populations. The addition and subtracting symbols reflect the positive

802   or negative effects, respectively, of the cv of the climatic variable to the phenotypic plasticity

803   values.

804

805   **Appendices**

806   Appendix A. Generalized linear mixed-effect models to fit the competition index.

807   Appendix B. Detailed description for climate variable selection.

808   Appendix C. Detailed description of the results from the linear mixed-effect models and

809   principal component analyses to select the climate variables of $clim_p$ and $clim_t$.

810   Appendix D. Linear mixed-effect model methodology to fit the tree height model for each

811   species.

812   Appendix E. Complementary description of the final linear mixed-effect models of each

813   species.

814

815

	4 years	8 years	16 years

P. nigra

(a)

(b) 0.7235, 0.7264, 0.7293

(c) 0.70710, 0.71095, 0.71480

(d) 0.65720, 0.67695, 0.69670

P. pinaster

(e) prec.dfj$_p$

(f) 0.8419, 0.8744, 0.9069

(g) 0.83470, 0.86655, 0.89840

(h) 0.8205, 0.8497, 0.8789

P. pinea

(i) prec.jja$_p$

(j) 0.8840, 0.8871, 0.8902

(k) 0.8704, 0.8717, 0.8730

(l) 0.8294, 0.8388, 0.8482
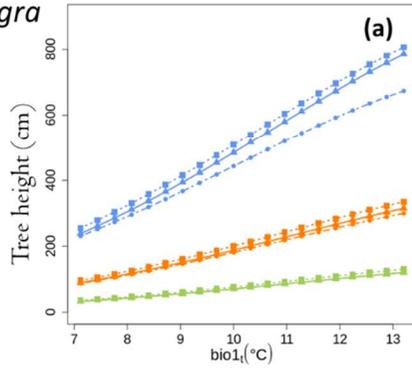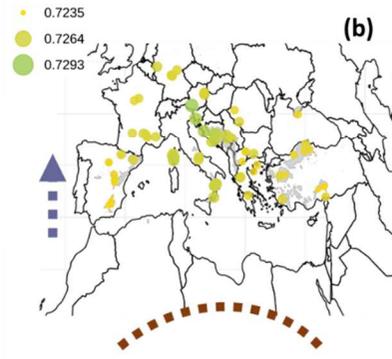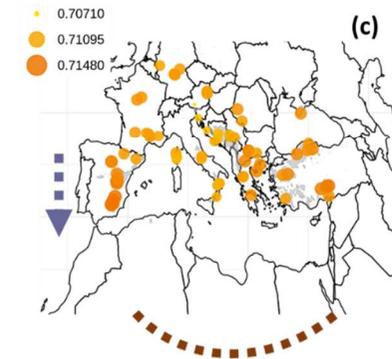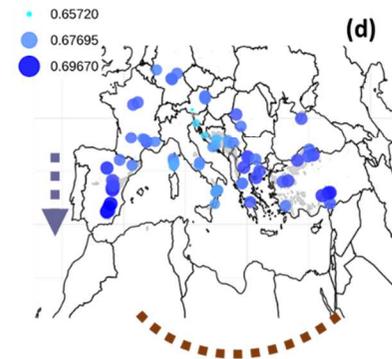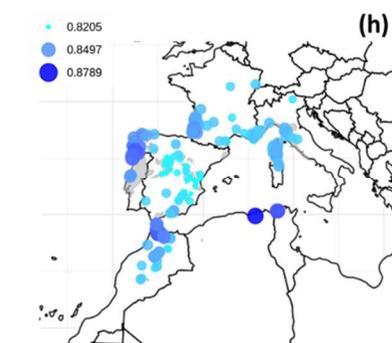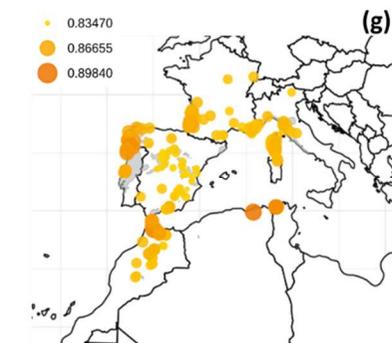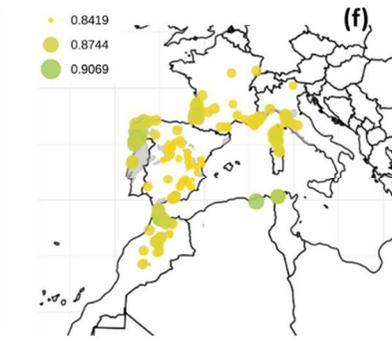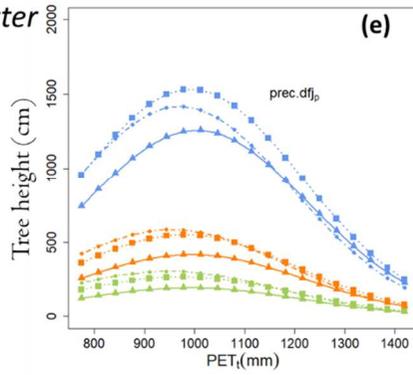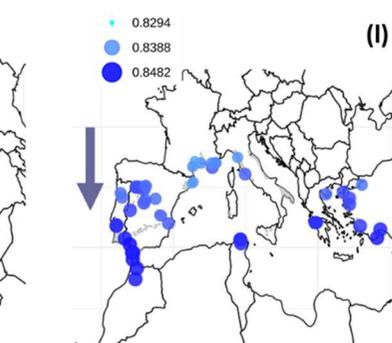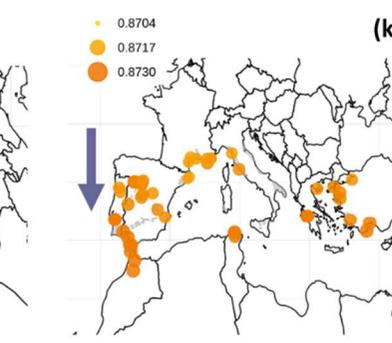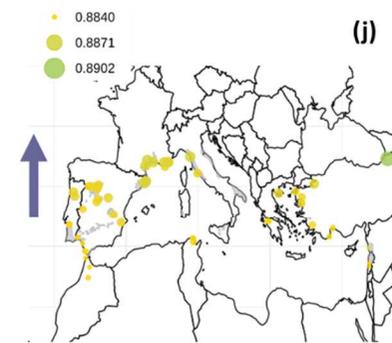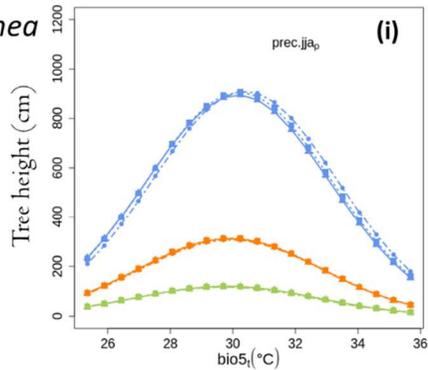
Populations' origin — High - ■- Aver -- ▲-- Low

1

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3 and Low in terms of $clim_p$ values) and for the three classes of age (4 years: green, 8 years: orange and 16 years: blue) for (a) *P. nigra*, (e) *P. pinaster*

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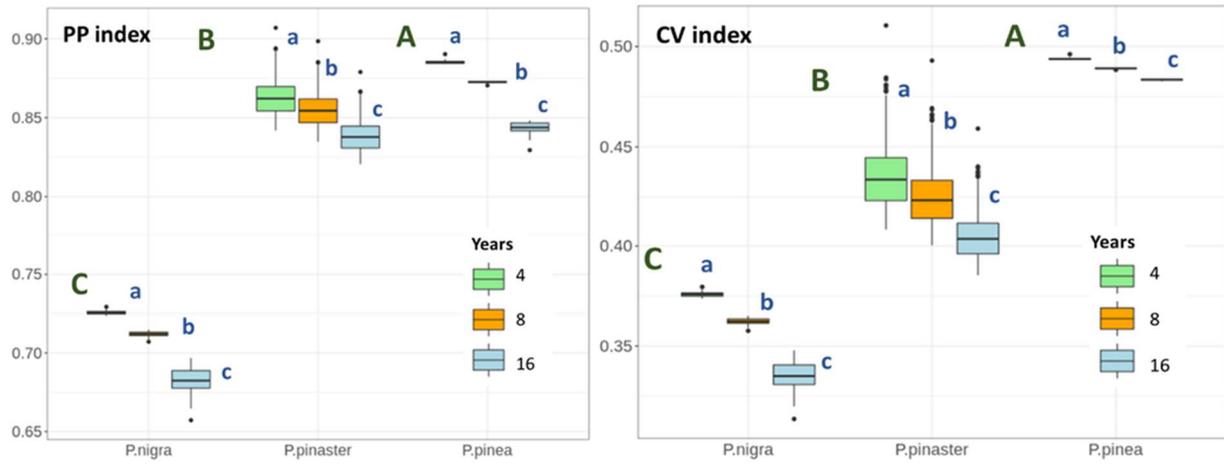
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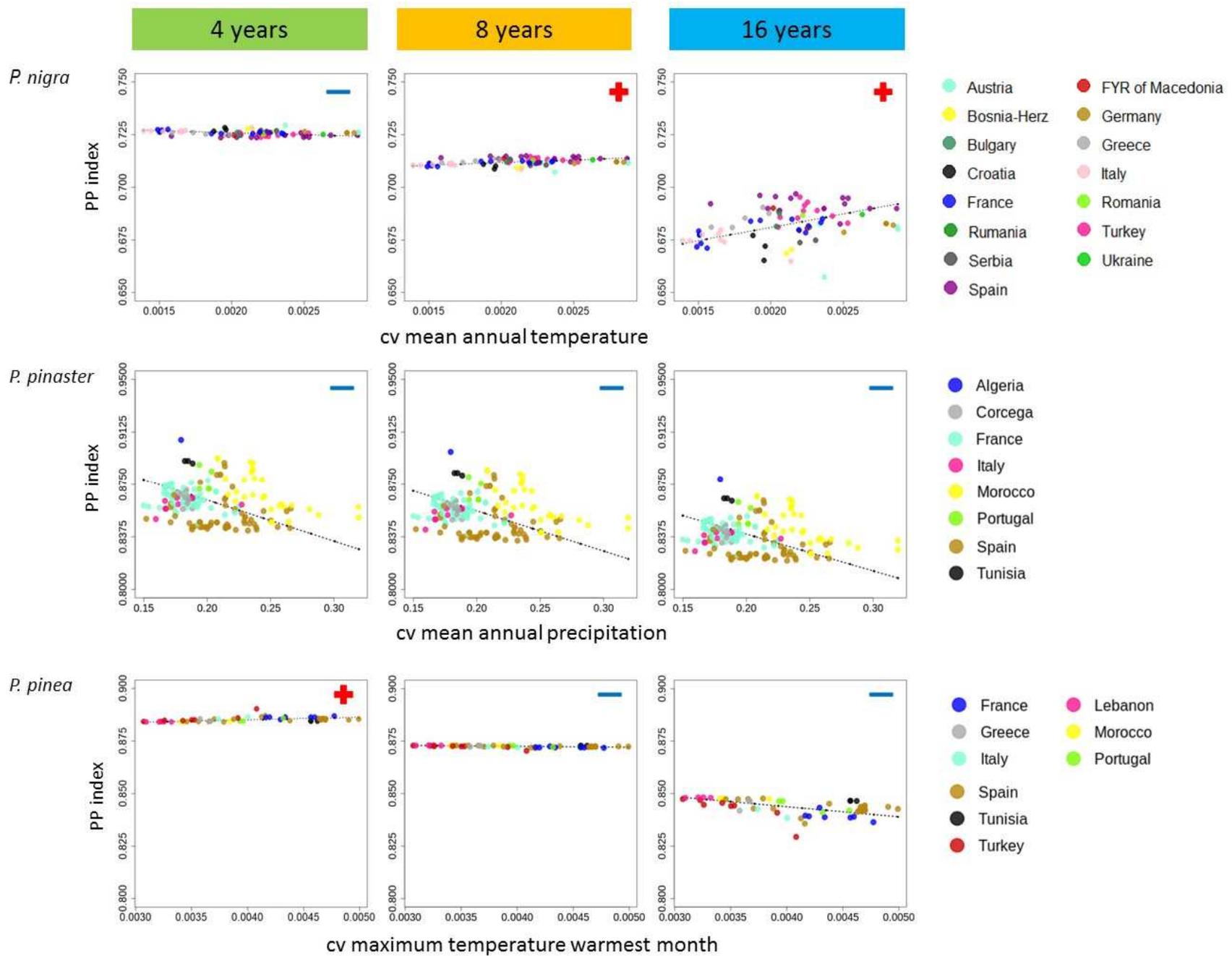
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17   The addition and subtracting symbols reflect the positive or negative effects, respectively, of the cv of the climatic variable to the

18   phenotypic plasticity values.

Phenotypic variation in tree height:

legacy at population origin

Climate variability

Population
Pop.1
Pop.2
Pop.3
Pop.4
Etc.

Time (from 1901 until trees are planted)

across species ranges

Pop.4

Pop.3

Pop.2

Pop.1

Level of phenotypic variation
(proxy of phenotypic plasticity)

across lifespan

4 y-old > 8 y-old > 16 y-old