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Adaptation and plasticity in aboveground allometry variation of four pine species along environmental gradients

Natalia Vizcaíno-Palomar, Inés Ibáñez, Santiago C. González-Martínez, Miguel A. Zavala & Ricardo Alía

Vizcaíno-Palomar, N. (natalia.vizcaino.palomar@gmail.com) [1,2]
Ibáñez, I. (iibanez@umich.edu) [3]
González-Martínez, S.C. (santiago.gonzalez-martinez@pierroton.inra.fr) [1,4,5]
Zavala, M.A. (ma.zavala@uah.es) [2]
Alía, R. (Corresponding author, alia@inia.es) [1,4]

[1] Department of Forest Ecology and Genetics, Forest Research Centre (INIA). Ctra. A Coruña, km 7.5, 28040 Madrid, Spain.

[2] Forest Ecology and Restoration Group, Department of Life Sciences, Science Building, Universidad de Alcalá, Campus Universitario, 28871 Alcalá de Henares (Madrid), Spain.

[3] School of Natural Resources and Environment, University of Michigan, Ann Arbor, MI 48109, USA443

[4] Sustainable Forest Management Research Institute, University of Valladolid-INIA, Avd. Madrid s/n, 34004, Palencia, Spain
[5] BIOGECO, INRA, Univ. Bordeaux, 33610 Cestas, France

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Abstract

Plant species aboveground allometry can be viewed as a functional trait that reflects the evolutionary trade-off between above- and belowground resources. In forest trees, allometry is related to productivity and resilience in different environments, and it is tightly connected with a compromise between efficiency-safety and competitive ability. A better understanding on how this trait varies within and across species is critical to determine the potential of a species/population to perform along environmental gradients. We followed a hierarchical framework to assess tree height-diameter allometry variation within and across four common European *Pinus* species. Tree height-diameter allometry variation was a function of solely genetic components –approximated by either population effects or clinal geographic responses of the population's site of origin–, and differential genetic plastic responses –approximated by the interaction between populations and two climatic variables of the growing sites, (temperature and precipitation)–. Our results suggest that, at the species level, climate of the growing sites set the tree height-diameter allometry of xeric and mesic species (*Pinus halepensis*, *P. pinaster and P. nigra*) apart from the boreal species (*P. sylvestris*), suggesting a weak signal of their phylogenies in the tree height-diameter allometry variation. Moreover, accounting for inter-population variability within species for the four pine species aided to: (i) detect genetic differences among populations in allometry variation, which in *P. nigra* and *P. pinaster* were linked to gene pools –genetic diversity measurements–; (ii) reveal the presence of differential genetic variation in plastic responses along two climatic gradients in tree allometry variation. In *P. sylvestris* and *P. nigra*, genetic variation was the result of adaptive patterns to climate, whilst in *P. pinaster* and *P. halepensis*, this signal was either weaker or absent, respectively; and (iii) detect a local adaptation response in the exponent of the tree height-diameter allometry relationship in two out the four species (*P. sylvestris* and *P.nigra*), as it was a function of populations' latitude and altitude variables. Our findings suggest that the four species have been subjected to different historical and climatic constraints that might have driven their aboveground allometry and promoted different life strategies.

Keywords: Bayesian modeling; Climatic and geographical clines, Environmental gradients; Functional trait; Iberian Peninsula; Intra-species variability; Provenance tests.

Introduction

Aboveground allometry is considered a functional trait that links the changes in total height to those in stem diameter and reflects the evolutionary outcome in plant species dynamics for above and belowground resources (Hallé, Oldeman & Tomlinson 1978; King 1996). Both height and stem diameter are tightly associated with species foraging and resource allocation strategy (Tilman 1988; Poorter *et al.* 2012): while tree height reflects a strategy for securing carbon profit via light capture (Moles *et al.* 2009), stem diameter is closely related to mechanical support and water-absorbing capacity (McMahon 1973; Niklas 1993; Bullock 2000). A finite set of allometric outcomes is then expectable, due to trade-offs in plant allocation strategies along resource gradients (sensu Tilman (1988)) or biomechanical and hydraulic constraints (e.g. Ryan & Yoder 1997; Chave *et al.* 2005; Mäkelä & Valentine 2006).

Tree height-diameter allometry has profound effects on species fitness and consequently on ecosystem structure. It correlates with bioclimatic variables (e.g. Aiba & Kohyama 1996; López-Serrano *et al.* 2005; King *et al.* 2006), and can change along biotic and abiotic gradients such as those for temperature, aridity and competition (e.g. Banin et al., 2012; Lines et al., 2012). However, intraspecific variation in allometry has usually been neglected and most studies have focused either on the species level or on the broad geographical scales (López-Serrano *et al.* 2005; Chave *et al.* 2005; Dietze, Wolosin & Clark 2008; Poorter *et al.* 2012; Lines *et al.* 2012; but see Vieilledent *et al.* 2010; Pretzsch & Dieler 2012, that considered individual variability). The extent and patterns of variation in inter-population genetic in tree height-diameter allometry still remains unclear. Those patterns could be as a result of adaptive or neutral genetic processes, such as past events e.g. migration, bottlenecks, drift, etc., at different scales (species, population or individual), of plastic responses to the environment, or by any combinations of them. Consequently, aboveground allometry emerges as a comprehensive and integrative trait in which the pattern of allocation variation within species could be driven by climate and inter-population genetic variation. A deep understanding of these interconnected levels of variability (species and populations) in tree height-diameter allometry is necessary to forecast the full potential of tree species to adapt and/or evolve under climate change conditions (e.g. Benito-Garzón *et al.* 2011; Valladares *et al.* 2014).

Common gardens experiments are established for testing genetic differences among populations grown under similar environmental conditions and generate valuable information for the study of intraspecific genetic variation (e.g. Matyas 1996; Alberto *et al.* 2013). Multi-locality common gardens, additionally, allow studying phenotypic plastic responses along environmental gradients and to identify genetic variation on them (i.e. population-environment interaction) and the adaptive value of those responses as well (i.e. correlations between the growing environments and local environments of population's origin).

In this study, we used total height and stem diameter –over bark– measured in multi-locality common garden tests to assess allometry relationships for the four most planted European pine species: *Pinus sylvestris* L., *P. nigra* Arnold, *P. pinaster* Aiton and *P. halepensis* Miller. The first two species (*P. sylvestris* and *P. nigra)* belong to the *Pinus* subsection that corresponds to Eurasian pines; and the last two species to the *Pinaster* subsection which relates to Mediterranean pines. Accordingly, these species display differentiated demographic backgrounds and genetic compositions resulting in a predictable pattern along temperature and water availability gradients across Europe (Richardson 1998; Tapias *et al.* 2004; Soto *et al.* 2010). We implemented a flexible log-linear model taking into consideration each species' population origin and associated geographic characteristics (to account for intraspecific genetic variation), and the climatic characteristics of the growing site (to account for the among-site variation). Correspondingly, we tested three hypotheses: (i) the patterns of height-diameter allometry variation in pines are driven by both the species and the inter-population variation; (ii) at the species level, tree allometry will vary depending on the climatic characteristics of the species, and specially with marked differences among Eurasian an Mediterranean species; (iii) inter-population variation in allometry could be the result of adaptation to local environments –namely climate and/or geographical variables of populations' site of origin– or historical events that took place in the past of the species. Testing these hypotheses will allow us to understand the underlying abiotic drivers that shape allometry variation at two interconnected levels, species and populations, and to identify the class of adaptive responses if existent. Understanding phenotypic integration of tree species responses along abiotic conditions could then assist in forecasting the performance of forest species and populations in the context of global warming.

Methods

Plant material and common garden provenance tests

Aboveground allometry was measured in multi-locality common garden provenance tests located in Spain for four pines species: *Pinus sylvestris*, *P. nigra*, *P. pinaster* and *P. halepensis*. Populations from the distribution range of the species, mostly from the Iberian Peninsula (Spain and Portugal), were sampled by collecting seed lots from at least 25 mother trees with a 50-meter separation distance. Plants originating from the seed lots were collected in different populations (22 for *P. sylvestris*, 23 for *P. nigra*, 52 for *P. pinaster* and 56 for *P. halepensis*), and established in comparative common garden provenance tests for each species (Fig. 1 and see Table S1 in Supporting Information).

Measurements were collected at 11 ± 1 years of age, depending on the common garden tests, for two variables: *height* (total height in cm, measured with a pole) and *dbh* (diameter at breast height [130 cm] in mm, measured with a caliper). A common age was chosen to minimize species differences along their ontogenies (López-Serrano *et al.* 2005), and avoid confusion of allometric changes due to size, known as 'passive or apparent plasticity' (Wright & Mcconnaughay 2002). We also selected a young age to minimize inter-population competition effects in the experimental design. A previous study using the same experiment setup as in the present research did not find either inter or intra population competition effects in any of the two variables measured (*height* and *dbh*) in 32-year-old *P. pinaster* individuals (Alía, Moro & Denis 2001).

In total, we used data from 4,853 *P. sylvestris* trees from 22 populations planted in 6 sites; 3,644 *P. nigra* trees from 23 populations in 8 sites; 9,976 *P. pinaster* trees from 54 populations in 4 sites; and 1,928 *P. halepensis* trees from 56 populations in 3 sites.

Climatic and geographical data

Each site was characterized by a set of 47 climatic variables: minimum, average and maximum mean monthly temperature, minimum and maximum average temperature of the coldest and warmest months and total and seasonal precipitation. As we lacked real climate data from weather stations, we estimated these variables based upon Gonzalo-Jiménez's (2010) climatic model for the Iberian Peninsula, with a 1-km^2 spatial resolution, from climate data gathered between 1951 and 1999 (see Appendix text S1 for further information).

According to both literature and exploratory analyses, we selected the subset of climatic variables at the growing sites most relevant to plant allometry for the four species. The selected variables were *MMT* (minimum average temperature of coldest month, ºC), and *AP* (annual precipitation, mm). Both *MMT* and *AP* affect physiological and growth processes of plant species in the Mediterranean region (Thompson 2005), and have been consistently used in previous studies (e.g. Wang *et al.* 2006; O'Neill & Nigh 2011; Leites *et al.* 2012). Moreover, these variables presented substantial correlation with *height* and *dbh* variables (see Table S3). Geographical variables of the populations' site of origin, such as latitude, longitude and altitude, are surrogates for environmental conditions, e.g. the amount of heat energy received relative to the sun angle, temperature, humidity, and solar radiation; and they can usually reflect adaptation patterns to local conditions (see Alberto *et al.* 2013). Climatic variables of the growing sites and geographic variables of the populations' site of origin were then standardized before analyses to ease comparison among variables in the model.

Although the number of growing sites is low (ranging between 3 and 8), they cover most of the natural climatic range associated with each species distributional range, including contrasting climates (Ruiz-Benito *et al.* 2013), (see Fig. S1).

Statistical models

We estimated tree height as a function of diameter by using three classic allometric functions (Linear, Power, and Gompertz), and two link functions (normal and log-normal) and implemented generalized linear models (GLMs). The best allometric model fitting the data was selected using the Deviance Information Criteria, DIC (Spiegelhalter *et al.* 2002). A power function with a log-normal link function was the best model for two out of the four species, and the second best model for the other two species (see Table S2). We selected a common allometric model, power function with a log-normal link, for the four species to facilitate parameter comparisons.

Based on this allometric model, we constructed a hierarchical model (Clark 2005, 2007). These models are more appropriate to connect and represent the biological hierarchy of the data, e.g. populations within species. To build the best final model, we considered several variations of the basic model (i.e. in Eq. 1), where a and c scaling parameters were constant, and they were estimated with different combinations of the variables associated with the growing sites and the origin of populations. The best final model structure was selected based on both biological relevance and the DIC criterion.

The final model estimated tree height allometry as a combination of climate at the growing site (*s*) and geographic characteristics at the origin site of the population (*p*).

Considering an individual *i*, from population *p* growing in growing site *s*, its height-diameter allometry was modeled as:

Likelihood: $\text{height}_i \sim \log \text{Normal}\,(H_i, \sigma^2)$

and the following process model:

$$H_i = \ln(a_{p(i),s(i)}) + c_{p(i)} \times dbh_i \qquad \text{Eq. 1}$$

where the scaling coefficient $ln(a_{p(i),s(i)})$ was estimated as:

$$\ln(a_{p(i),s(i)}) = \alpha_{1p} + \alpha_{2p} \times MMT_s + \alpha_{3p} \times AP_s \qquad \text{Eq. 2}$$

and the scaling exponent, $c_{p(i)}$, was estimated as:

$$c_{p(i)} = \beta_1 + \beta_2 \times LAT_p + \beta_3 \times ALT_p \qquad \text{Eq. 3}$$

Tree height-diameter allometry, therefore, is the outcome result of population genetic effects on the basal height, parameterized in α_{1p}; plus a genetic (population) clinal geographical pattern of the scaling exponent on latitude and altitude ($\beta_2 \times LAT_p$,$\beta_3 \times ALT_p$), and of genetic differential plastic responses along temperature and or precipitation gradients of the growing site ($\alpha_{2p} \times MMT_s$, $\alpha_{3p} \times AP_s$). Because all explanatory variables were standardized, parameter α_{1p} was the allometric curve's intercept at average climate conditions of across all growing sites. A summary of model parameters, significance, and insights that can be assessed on each one is shown in Figure 2.

Model parameters estimation and posthoc comparisons

Parameters were estimated following a Bayesian approach highly suited for hierarchical analyses (Gelman & Hill 2007). Each of the population level parameters, α_{*p}, was estimated from a species-level prior normal distribution, with hyperparameters μ_* and $\sigma_{\alpha*}^2$, $\alpha^*_p \sim N(\mu_*, \sigma_{\alpha*}^2)$, estimated from non-informative prior distributions $\mu_* \sim N$ (0,

1000) and $\sigma_{\alpha*}$~Uniform (0, 100). These species-level parameters μ_* and $\sigma_{\alpha*}^2$ would correspond *sensu stricto* to an inter-population average among the studied populations. However, we refer to these parameters *sensu lato* as representative of a species proxy response. Note that for the scaling coefficient we have referred in Eq. 2 to populations' parameters to enhance comprehension of the full scope of the relationship, instead of including the species' parameters.

Parameters β_* were also estimated from non-informative prior distributions, β_* ~N (0, 1000). Variance associated with the individual random effects was estimated as $1/\sigma^2$ ~ Gamma (0.01, 0.01). As standard deviation of residual errors around a fitted power function might increase with diameter, we tested whether the residuals were a linear function of diameter, as recommended in Lines et al. (2012). However, our residuals did not show this trend, so we considered unnecessary to account for diameter size in the estimation of the variance.

We formally tested marginal significant intraspecific genetic differences in α_p^* for each species by computing all pairwise combinations of population differences accounting for the 95% credible interval, CI, of the estimated parameter distribution (e.g. intraspecific genetic differences in α_p^* = $\alpha*_{p_A} - \alpha*_{p_B}$, being A and B two populations of a specific pine species), while the rest of variables were kept to their mean values in the range, that is why we refer to these differences as 'marginal'. Two populations were significantly different if zero was not included in the credible interval around their difference. Additionally, we quantified the level of marginal intraspecific genetic differences as the percentage of the total number of significant pairwise comparisons relative to the total number of pairwise comparisons within species. Finally, to end the characterization of intraspecific genetic variability within species, we provided the range of variability among populations within species as the standard deviation of $\alpha*_p$, i.e. the set of parameters estimated for each population.

Models were run in OpenBUGs (version 3.2.2 rev 1063) (Thomas *et al.* 2006). Three chains were run for ~50,000 iterations and parameters convergence was reached after ~25,000 iterations. After the burn-in period, chains were thinned (every 100) to reduce autocorrelation, then posterior parameter values (mean and 95% credible intervals) were calculated. Plots of predicted vs. observed values were also used to evaluate model fit (unbiased models having a slope of one and R^2 values indicating goodness-of-fit). A slope parameter was considered to be statistically significant when the 95% credible interval (CI) did not include zero. Population level parameters were considered significantly different when their 95% CI did not overlap (or the 95% CI around their difference did not include zero).

Species' adaptive patterns in height-diameter allometry variation.

We tested whether variation in the α_p^* parameters was the result of neutral and/or adaptive responses to local environments, by using two different approaches. First, to assess the influence of neutral responses on α_p^* parameters of allometry, we tested the influence of previously defined gene pools groups for each species on α_p^* parameters. Gene pools are proxies of genetic relationships among populations, indicating common demographic or evolutionary factors. In *P. sylvestris*, *P. pinaster* and *P. halepensis*, gene pool groups were defined using molecular markers in Robledo-Arnuncio et al. (2005) and in Bucci *et al.* (2007). In *P. nigra*, we lacked information based on molecular markers; hence populations were grouped by sub-species. One-way ANOVA was used to detect the existence of association between α_p^* parameters and groups, and post-hoc comparisons with a HSD Tukey's test were employed. When homogeneity and normality assumptions were not reached, non-parametric Kruskal-Wallis test and post-hoc comparisons with a Nemenyi test, corrected for ties if necessary, were used. Second, to identify the influence of local environments –namely climate and/or geographical position of populations' site of origin– on tree allometry variation; we tested the existence of climatic or geographical clines due to local adaptations in phenotypic plasticity. More specifically, we computed Pearson correlation coefficients (ρ) between α_p^* parameters and climate and geographical characteristics of the populations' site of origin.

Results

Patterns of height-diameter allometry variation across and within species

The four final models produced unbiased estimates of *height* with high R^2 of observed *vs* predicted values (0.90 in *P. sylvestris*, 0.91 in *P. nigra,* 0.85 in *P. pinaster* and 0.89 in *P. halepensis*).

Pinus pinaster had the lowest intercept value, measured by hyperparameter μ_1, and it did not overlap with the other three species. *P. nigra* and *P. sylvestris* had intermediate but overlapping values, while *P. halepensis* had the highest value and did not overlap with any of the other pine species (Table 1). The intraspecific variability, standard deviation of α_{1p}, also varied among species. *P. pinaster* displayed the greatest value, followed by *P. nigra*, *P. sylvestris* and *P. halepensis* (Table 1). This intraspecific variability can also be visualized in Figure S2. Moreover, there was significant intraspecific genetic variation in α_{1p} in all species, measured by the number of significant pairwise comparisons within species relative to the total number: *P. pinaster* was the species with the highest percentage of significant differences (50.24 %); followed by *P. nigra* (40.32%), *P. sylvestris* (31.17%) and *P. halepensis* (17.21%).

Temperature (*MMT*) of the growing site influenced tree height allometry, being this hyperparameter, μ_2, statistically significant and positive in three out of the four species, and significant but negative in *P. sylvestris* (Table 1). Moreover, we found evidence of inter-population genetic differentiation in phenotypic plasticity to temperature (*MMT*) in three out of the four species (except *P. halepensis*). The four species showed some degree of intraspecific genetic variability, *P. sylvestris* having the greatest standard deviation, followed by *P. pinaster*, *P. nigra* and *P. halepensis*. Specifically, the level of significant intraspecific genetic variation varied according to each species. Thus, *P. sylvestris* displayed the greatest level of genetic differences in plasticity in response to *MMT* (38.10 %) among the populations tested, followed by the other two species: *P. nigra* (9.88%) and *P. pinaster* (9.57%). All these results should be considered based on the total of populations tested. This intraspecific genetic variability can also be visualized in Figure S3.

Annual precipitation (*AP*) also influenced tree height allometry. Values for hyperparameter μ_3 were statistically significant and negative in three out the four species, but positive in *P. sylvestris*. The estimated values for *P. sylvestris* and *P. halepensis* did not overlap, but the pairs composed by *P. nigra* and *P. pinaster*, and *P. pinaster* and *P. halepensis* did (Table 1). Similarly, we found intraspecific genetic differences in phenotypic plasticity to rainfall (*AP*) in three out of four species, the exception again being *P. halepensis*. Furthermore, the four pine species presented some degree of intraspecific variability. *P. sylvestris* and *P. pinaster* presented similar degrees, followed by *P. nigra* and *P. halepensis*, (Table 1). The level of significant intraspecific genetic variation was greatest in *P. sylvestris* (29.87%), followed by *P. pinaster* (3.60%) and *P. nigra* (2.77%). This intraspecific variability can also be visualized in Figure S4.

In three out the four species, the effects of *AP* on the tree height-diameter relationship and also the intraspecific genetic variability were smaller than those reported in response to *MMT*; specifically, between ca. 2 and 3.5-folds greater for *P. nigra, P. halepensis* and *P. pinaster* –in an increasing order–. Interestingly, the opposite effect was found in *P. sylvestris* –the effect of *AP* was ca. 2.5 folds greater than *MMT*–.

Species' adaptive patterns in height-diameter allometry variation

Overall, we found that tree height allometry variation was the result of adaptive responses to either local environments –climate and geographical sites of origin– or to past historical events in the demography of species. First, we found a significant geographical cline, i.e. an association between the scaling exponent parameter (c_p) and the latitude of origin for two of the four pine species (*P. sylvestris* and *P. nigra*), but not for the other two, more xeric, species (*P. pinaster* and *P. halepensis*) (Table 1). Second, gene pool groups were significantly associated with α_{1p} values just in *P. pinaster* and *P. nigra* ($p < 0.001$ and $p < 0.05$, respectively), but not in the two others (Table 2).

Third, we found chiefly stronger local environment –namely climate and geographical position of populations' site of origin– associations with α_{1p} parameters compared to α_{2p} and α_{3p}. Interestingly, P. *halepensis* was the only species that lacked any type of relationship, suggesting the inexistence of climate adaptive responses in tree allometry variation. Specifically, α_{1p} values were significantly correlated ($p < 0.05$) to different climatic variables of population's site of origin (Table 3). *P. sylvestris* with altitude ($\rho = 0.56$) and annual precipitation ($\rho = 0.54$); *P. nigra*, in general, with minimum average monthly temperature (ranging from $\rho = 0.45$ to 0.60); and, weaker than the previous two, *P. pinaster* with spring precipitation ($\rho = 0.28$) and mean temperature of the warmest month ($\rho = -0.28$). Parameters α_{2p} and α_{3p} were significantly correlated to climatic variables of populations' sites of origin ($p < 0.05$); *P. sylvestris*, *P. nigra* and *P. pinaster* displaying significant correlations between α_{2p} and climate, although the associations were weaker in the last species. Finally, we only found significant and positive correlations between α_{3p} and related temperature variables in *P. sylvestris* (Table 3).

Discussion

We addressed inter-population tree height-diameter allometry variation across precipitation and temperature gradients of the four most planted pine species in Spain, i.e. tree height-diameter allometry variation was accounted at two interconnected levels, species and population. Additionally, we found that local adaptation and past historical events of the species were associated to inter-population allometry variation, except for *P. halepensis*, the most xeric species among the four. We employed a hierarchical approach to better understand the contributions of the species' genetic variation, their demographic genetic background and their phenotypic plasticity, in their responses to environmental variability.

Patterns of height-diameter allometry variation across and within species

This is the first time, to our knowledge, that the patterns of aboveground allometry across climatic gradients have been described including intraspecific variation from a genetic perspective. The species-level parameters related to allometry (hyperparameters μ_* and β_*, Figure 2) did not overlap among species in most comparisons, reflecting the existence of evolutionary species-specific allocation strategies to cope with the current environment, although revealing an unclear association with their phylogeny, because *P. nigra* behaved more like *P. halepensis* and *P. pinaster* than like *P. sylvestris*.

In general, *P. sylvestris* showed the opposite pattern in regards to aboveground allometry variation across precipitation and temperature gradients with respect to the other three species. Aboveground variation was also more responsive to changes in the minimum average temperature of the coldest month, *MMT*, than to changes in annual precipitation, *AP* (excluding again *P. sylvestris*). This is contrary to expectation as Iberian forests are strongly constrained by water availability (Gómez-Aparicio *et al.* 2011; Ruiz-Benito *et al.* 2013). We hypothesize that mesic and xeric pine species could be more limited by low temperatures than by water shortage, since they may have developed adaptive mechanisms to cope with drought stress, such us tight stomatal control, or specific wood anatomy traits such as thick cell walls, thick pit membrane, narrow lumens or different root hydraulic resistance (Yastrebov 1996; Tyree & Zimmermann 2002; García Esteban *et al.* 2009; Zuccarini *et al.* 2015). Yet our data did not allow us to explore all potential interactions, e.g. too cool-too wet; too warm-too wet that are likely to shape evolutionary responses in these species and populations.

Consistently with previous studies, in three out of the four pine species, taller heights at a given size are found under warmer conditions (Lines *et al.* 2012), except for *P. sylvestris*. Warmer conditions during the cold season might allow a higher photosynthetic capacity, resulting in a higher rate of carbon assimilation (Way & Oren 2010), and hence taller heights. Yet *P. sylvestris* showed the opposite trend, suggesting a lack of responsiveness to warmer winters. A similar result was reported by Reich & Oleksyn (2008) in a regional study in Northern Europe (latitude from 46º to 68º N). They observed that *P. sylvestris* responses to climate differed between northern and southern populations: while in southern populations height decreased as temperature increased, the opposite was observed in northern populations. It was suggested that, at least for this temperate-boreal species, warmer temperatures –at its warmer range– might rather enhance heat stress and heat-induced moisture stress than alleviate cold stress.

Tree height allometry variation across the precipitation gradient resulted species-specific and diverse. *P. sylvestris* is expected to decrease its height at given size under drier conditions, a common pattern found in many parts of the world, e.g. Méndez-Alonzo *et al.* (2008). This variation has often been attributed to the changing hydraulic structure of vessels in drought-prone areas. The opposite, however, was observed for *P. halepensis*. Periods of soil moisture saturation and flooding may act as stressors in arid-climate forests by reducing tree height (Rodríguez-González *et al.* 2010). Also higher precipitation levels in some regions could imply poorer soil quality, because of increased runoff and nutrient leaching. However, as we do not have these measurements, we cannot confirm its potential influence. Intermediate patterns in tree allometry variation were shown for *P. pinaster* and *P. nigra*¸ which displayed negligible variation along the precipitation gradient tested. Lines *et al.* (2012) found a clear pattern of allometric variation across species along the studied precipitation gradient, although not within species. That finding together with ours suggest that tree height-allometry variation could have a very conservative performance across precipitation gradients. This latter would be in agreement the results presented in Table 1. Here, the estimated credible intervals for the hyperparameters in *P. pinaster* and *P. nigra* were very close to containing zero. This is somehow reflecting the almost lack of influence of precipitation on tree height-diameter allometry variation.

Species’ adaptive patterns in height-diameter allometry variation

According to our findings, inter-population tree height allometry variation was the result of local adaptation (Table 3). In addition, for *Pinus nigra* and *P. pinaster*, the demographic history of the species associated to distinct neutral gene pools was also important (as they reflect past events along the species’ history, such as genetic bottlenecks, founder effects, drift, etc.; Bucci *et al.* 2007; Soto *et al.* 2010; Jaramillo-Correa *et al.* 2015) (Table 2). Thus, in these two species, gene pool signals correlate with its allometry – its phenotype–, and therefore, such gene pools could be further used for the study of different evolutionary processes on phenotype variation, although the delineated groups were appreciably different compared to those based on DNA data (Afzal-Rafii & Dodd 2007; Bucci *et al.* 2007). Absence of this signal in *P. sylvestris* could be partly explained by a greater influence from local environments relative to species historical background, as it is reflected by significant correlations between α_{*p} and local population climate. In contrast, *P. pinaster* and *P.nigra* presented weak signals of adaptation to climate, specifically in plastic responses to temperature. Finally, *P. halepensis* represented a different case; its null degree of genetic variation, in any of the parameters of the model, agrees with the fact that the species’ European western populations are genetically uniform (Soto *et al.* 2010), due to a relatively recent long-range colonization from its ancestral range in the eastern Mediterranean Basin (Grivet *et al.* 2009).

The clear latitudinal variation in the scaling exponent parameter in *P. sylvestris* and *P. nigra* reveals a consistent regional correlation in tree allometry and photoperiod. Previous studies along latitudinal gradients have also found a genetic cline of adaptation (e.g. northern populations set buds and hardened earlier, and presented lower growth rates than the southern ones; see Alberto *et al.* 2013 and references therein). In any case, the lack of latitudinal clines in *P. halepensis* and *P. pinaster* could be explained to either insufficient span in our data or to a real lack of latitudinal variability. Interestingly, this is the first time that adaptive patterns have been shown for a composite trait such as tree height allometry. Our results confirm that this trait and its confined variation may be under natural selection control and consequentially play an important role in both the adaptation and acclimation potential of tree species to future conditions.

In conclusion, these four pine species are a heterogeneous group with a recognized ability to adapt to extremely variable environments. Our findings support the eco-evolutionary knowledge we already have about them, but nonetheless reveal that height-diameter allometry variation patterns have developed under different natural selection pressures, despite the study species sharing a sizeable part of their distribution area in the studied region. This might have resulted in species, such as *P. halepensis*, where phenotypic plasticity is more important than genetic variation; while for others, e.g. *P. pinaster*, genetic variation and local adaptation might be more relevant. Together, local environments – at the origin– and current growing conditions outline the likely possible outcomes of integrated phenotypes.

The full potential of forest resilience and resistance along new temperature and aridity gradients, i.e. climate-change driven, would depend on local adaptation and levels of phenotypic plasticity of the populations. Our results point that considering both the species specific and population ecological and historical background is key for assessing likely population responses to environmental variation

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Author contributions

N.V.P., M.A.Z., S.C.G.M. and R.A. conceived this study; N.V.P. and I.I. analysed the data; all authors contributed to the writing of the manuscript.

Data accessibility

All the data used is available in the Database on Genetic trials GENFORED (www.genfored.es) upon request, and also it is in process of submitting into the CitaREA repository (http://citarea.cita-aragon.es/citarea/?locale=en). Identificators for the data will be available before publication.

Table 1. Parameter estimates from the selected best model. The table gathers information of two interconnected levels of hierarchy, species and populations. The parameters μ_* and β_* make reference to the species, and α_{*p} to populations within species. The overall species response, i.e. μ_* and β_* posterior mean estimates and 95% credible intervals in square brackets [,] are given. The range of parameter values among populations within species, i.e. posterior mean estimates of α_{*p}, are shown in square brackets, the lowest value is separated from the highest one by three dots […]. **Bold** numbers indicate that fixed-effect coefficients were statistically significant (i.e. 95% CI does not include zero). Letters indicate comparison and different letters indicate differences among species for each of the parameters when statistically significant.

	P. sylvestris	*P. nigra*	*P. pinaster*	*P. halepensis*

$ln(a_{p,s})$	Intercept: μ_1	**4.143** b	**4.121** b	**3.056** c	**4.344** a
		[4.123, 4.126]	**[4.093, 4.148]**	**[3.023, 3.088]**	**[4.302, 4.385]**
	α_{1p}	[4.107 ... 4.229]	[4.047 ... 4.198]	[2.907 ... 3.170]	[4.281 … 4.396]
	sd(α_{1p})	0.028	0.039	0.054	0.024
	MMT: μ_2	**-0.030** d	**0.037** c	**0.086** b	**0.158** a
		[-0.049, -0.011]	**[0.026, 0.049]**	**[0.072, 0.100]**	**[0.143, 0.172]**
	α_{2p}	[-0.120 … 0.026]	[0.014 … 0.063]	[-0.002 ... 0.169]	[0.143 … 0.174]
	sd(α_{2p})	0.032	0.011	0.026	0.007
	AP: μ_3	**0.080** a	**-0.0184** b	**-0.023** bc	**-0.049** c
		[0.070, 0.095]	**[-0.028, -0.009]**	**[-0.036, -0.009]**	**[-0.064, -0.035]**
	α_{3p}	[0.043 ... 0.128]	[-0.032 ... 0.000]	[-0.059 … 0.032]	[-0.053 … -0.043]
	sd(α_{3p})	0.019	0.007	0.018	0.002
c_p	Intercept: β_0	**0.426** b	**0.412** bc	**0.700** a	**0.397** c
		[0.416, 0.431]	**[0.405, 0419]**	**[0.691, 0.707]**	**[0.375, 0.409]**
	LAT: β_1	**0.016** a	**0.010** ab	0.005	0.003
		[0.007, 0.026]	**[0.002, 0.017]**	[-0.001, 0.012]	[-0.003, 0.008]
	ALT: β_2	-0.006	-0.004	-0.007	-0.002
		[-0.015, 0.004]	[-0.011, 0.004]	[-0.013, 0.000]	[-0.007, 0.004]

Table 2. A) Summary of one-way ANOVAs to test gene pool effects on α_{*p}. When a non-parametric test was used, it is shown by the symbol $^{\approx}$. B) Post-hoc comparisons among gene pools adjusted by Tukey's HSD for *P. nigra* and *P. pinaster*. Different letters indicate differences among gene pools.

A)

Species	Parameter	F / K	P-value
P. sylvestris	α_{1p}	0.60	n.s.
	α_{2p}	0.57	n.s.
	α_{3p}	0.57	n.s.
P. nigra	α_{1p}	6.95	**
	α_{2p}	7.20$^{\approx}$	n.s.
	α_{3p}	2.53$^{\approx}$	n.s.
P. pinaster	α_{1p}	12.43	***
	α_{2p}	14.23$^{\approx}$	n.s.
	α_{3p}	3.84$^{\approx}$	n.s.
P. halepensis	α_{1p}	1.07	n.s.
	α_{2p}	0.44	n.s.
	α_{3p}	0.08	n.s.

B)

	Gene pools	α_{1p}	**sd**	
P. nigra				
	spp. *laricio*	4.15	0.04	a
	spp. *salzmannii*	4.12	0.01	ab
	spp. *dalmatica*	4.08	*	ab
	spp. *nigra*	4.06	0.02	b
P. pinaster	Morocco	3.11	0.00	a
	Atlantic Iberian	3.10	0.02	a
	Eastern Spain	3.06	0.03	ab
	Southern Spain	3.06	0.05	abc
	Corsica	3.05	0.00	abc
	Central Spain	3.02	0.03	bc
	Italy	2.95	*	cd
	Eastern North Africa	2.91	0.00	d

* only one datum, standard deviation was not estimated.

Table 3. Heat map for Pearson's correlation coefficients, ρ, between α_{*p} and climate variables from the populations' sites of origin. Dark grey indicates high positive correlation coefficients, light grey indicates high negative, and white color indicates low. Bold numbers mean significant correlations at $p < 0.05$.

	P. sylvestris			*P. nigra*			*P. pinaster*			*P. halepensis*		
	α_{1p}	α_{2p}	α_{3p}	α_{1p}	α_{2p}	α_{3p}	α_{1p}	α_{2p}	α_{3p}	α_{1p}	α_{2p}	α_{3p}
Latitude	**-0.45**	0.14	0.19	-0.05	-0.24	-0.09	**-0.48**	0.03	-0.07	0.20	0.17	-0.04
Longitude	**-0.45**	-0.02	0.11	-0.29	0.22	0.37	0.00	0.09	0.08	0.03	-0.04	0.00
Altitude	**0.56**	-0.17	-0.29	0.06	-0.23	-0.31	0.16	**-0.33**	0.01	0.01	0.02	0.07
MMTJan	-0.03	0.29	0.23	**0.61**	**0.42**	0.16	-0.07	**0.27**	0.01	0.03	-0.05	-0.17
MMTFeb	0.00	0.31	0.20	**0.54**	0.34	0.13	-0.05	0.25	0.02	0.02	-0.06	-0.17
MMTMar	-0.21	0.36	0.32	**0.45**	0.31	0.17	-0.06	0.25	0.00	0.02	-0.06	-0.15
MMTApr	**-0.48**	0.37	0.38	0.34	0.22	0.14	-0.07	0.20	-0.01	0.06	-0.01	-0.16
MMTMay	**-0.53**	0.40	0.41	0.32	0.18	0.14	-0.13	0.18	0.00	0.06	-0.06	-0.18
MMTJun	**-0.52**	**0.44**	**0.44**	0.33	0.21	0.12	-0.16	0.13	-0.03	0.06	-0.07	-0.22
MMTJul	**-0.48**	**0.53**	**0.47**	**0.45**	0.23	0.10	-0.20	0.05	-0.04	0.06	-0.11	-0.22
MMTAug	**-0.43**	**0.56**	**0.46**	**0.48**	0.25	0.11	-0.22	0.04	-0.07	0.09	-0.06	-0.20
MMTSep	-0.38	**0.50**	0.39	**0.51**	0.35	0.17	-0.19	0.16	-0.04	0.06	-0.04	-0.16
MMTOct	-0.30	**0.46**	0.40	**0.55**	0.36	0.19	-0.16	0.21	-0.04	0.07	-0.01	-0.14
MMTNov	-0.32	0.42	0.37	**0.57**	0.35	0.18	-0.09	0.24	0.00	0.09	-0.01	-0.15
MMTDec	-0.17	0.30	0.26	**0.59**	0.38	0.18	-0.06	**0.27**	0.01	0.06	-0.04	-0.18
MWTJan	-0.02	**0.44**	0.33	0.33	0.29	0.07	0.10	0.16	-0.02	-0.07	-0.13	-0.14
MWTFeb	-0.17	**0.46**	0.40	0.17	0.21	0.07	0.01	0.14	-0.04	-0.15	-0.16	-0.13
MWTMar	**-0.44**	**0.53**	**0.51**	-0.05	0.10	0.08	-0.06	0.06	0.01	-0.25	-0.20	-0.08
MWTApr	**-0.59**	**0.43**	**0.48**	-0.17	-0.01	0.05	-0.13	0.04	-0.02	-0.16	-0.10	-0.05
MWTMay	**-0.63**	**0.47**	**0.46**	-0.23	-0.13	-0.05	-0.20	-0.09	0.02	-0.18	-0.12	-0.10
MWTJun	**-0.57**	**0.54**	**0.52**	-0.21	-0.15	-0.09	-0.15	-0.14	0.01	-0.25	-0.11	-0.04
MWTJul	-0.23	**0.48**	0.37	-0.15	-0.15	-0.13	-0.15	-0.21	0.03	-0.25	-0.10	0.02
MWTAug	-0.20	**0.52**	0.39	-0.11	-0.17	-0.14	-0.14	-0.15	0.01	-0.25	-0.08	0.02
MWTSep	-0.37	**0.53**	**0.43**	-0.05	-0.07	-0.06	-0.14	-0.06	0.01	-0.24	-0.16	-0.06
MWTOct	-0.33	**0.55**	**0.50**	0.04	0.04	0.01	-0.15	0.11	0.00	-0.17	-0.08	-0.09
MWTNov	-0.16	**0.50**	0.42	0.28	0.16	0.05	-0.05	0.20	0.00	-0.06	-0.05	-0.11
MWTDec	-0.09	**0.47**	0.40	0.39	0.30	0.11	0.06	0.23	-0.03	-0.01	-0.13	-0.17
MTJan	-0.02	0.41	0.31	**0.50**	0.38	0.13	0.01	0.23	-0.01	-0.02	-0.09	-0.17
MTFeb	-0.10	**0.43**	0.34	0.37	0.29	0.10	-0.03	0.21	-0.01	-0.06	-0.12	-0.17
MTMar	-0.37	**0.49**	**0.46**	0.18	0.21	0.13	-0.07	0.18	0.00	-0.11	-0.13	-0.15

MTApr	**-0.56**	0.42	**0.45**	0.06	0.10	0.09	-0.12	0.14	-0.02	-0.03	-0.05	-0.13
MTMay	**-0.61**	**0.45**	**0.45**	0.00	0.00	0.03	-0.20	0.06	0.01	-0.05	-0.10	-0.17
MTJun	**-0.57**	**0.51**	**0.50**	0.01	0.00	-0.01	-0.19	-0.02	0.00	-0.10	-0.11	-0.18
MTJul	-0.42	**0.59**	**0.50**	0.07	-0.01	-0.06	-0.21	-0.13	0.00	-0.15	-0.16	-0.16
MTAug	-0.35	**0.61**	**0.48**	0.13	-0.02	-0.06	-0.22	-0.08	-0.03	-0.11	-0.11	-0.15
MTSep	-0.41	**0.58**	**0.46**	0.22	0.12	0.05	-0.21	0.06	-0.02	-0.07	-0.11	-0.16
MTOct	-0.34	**0.56**	**0.50**	0.33	0.22	0.11	-0.18	0.18	-0.02	-0.02	-0.04	-0.13
MTNov	-0.26	**0.53**	**0.44**	**0.47**	0.28	0.12	-0.08	0.24	-0.01	0.03	-0.03	-0.14
MTDic	-0.14	**0.44**	0.37	**0.52**	0.36	0.15	0.00	0.26	-0.01	0.03	-0.08	-0.18
AP	**0.54**	-0.23	-0.20	-0.13	-0.17	-0.07	0.23	**0.40**	0.06	0.19	0.21	0.20
WintP	**0.45**	-0.33	-0.22	0.27	-0.20	-0.22	0.24	**0.40**	0.05	0.09	0.26	0.17
SpringP	**0.58**	-0.36	-0.31	-0.12	-0.17	-0.06	**0.28**	**0.35**	0.06	0.09	0.18	0.25
SumP	-0.17	0.00	0.11	**-0.52**	-0.04	0.17	0.18	0.07	0.03	0.12	0.01	0.08
AutP	**0.52**	-0.27	-0.14	0.16	0.04	-0.08	0.21	**0.34**	0.05	0.24	0.08	0.02
MAT	-0.39	**0.54**	**0.47**	0.25	0.17	0.07	-0.14	0.13	-0.01	-0.04	-0.11	-0.17
WT	**-0.43**	**0.57**	**0.47**	0.08	-0.02	-0.06	**-0.28**	-0.03	-0.01	-0.09	-0.15	-0.17
MWT	-0.21	**0.45**	0.35	-0.15	-0.16	-0.13	-0.14	-0.19	0.04	-0.22	-0.13	0.00
MT	0.00	0.40	0.30	**0.48**	0.37	0.12	-0.03	**0.32**	-0.02	-0.01	-0.12	-0.17
MMT	-0.01	0.30	0.24	**0.59**	0.41	0.15	-0.07	**0.27**	0.01	0.03	-0.07	-0.18

MMT# is the mean minimum temperature of the month #; **MWT#** is the mean maximum temperature of the month #; **MT#** is the mean temperature of the month #; **WintP** is total winter precipitation; **SpringP** is total spring precipitation; **SumP** is the total summer precipitation; **AutP** is total autumn precipitation; **AP** is the annual precipitation; **MAT** is the mean annual temperature; **WT** is the mean temperature of the warmest month; **MWT** is the mean maximum temperature of the warmest month; **MT** is the mean annual temperature; and **MMT** is the mean minimum temperature of the coldest month.

Figure legends

Figure 1. Common garden sites (Site, filled symbols), and population's sites of origin (Population, unfilled symbols) are represented in the map. Each pine species is represented in a different symbol Ps: *P*. sylvestris and it is represented by a circle; Pn: *P*. *nigra*, it is represented by a star; Pp: *P*. *pinaster* by a square, and Ph: *P*. *halepensis* by a triangle.

Figure 2. Summary information of the estimated parameters in the final tree height-diameter allometry model. We have described each parameter attending to its hierarchy, its significance and the set of research questions that can be addressed.

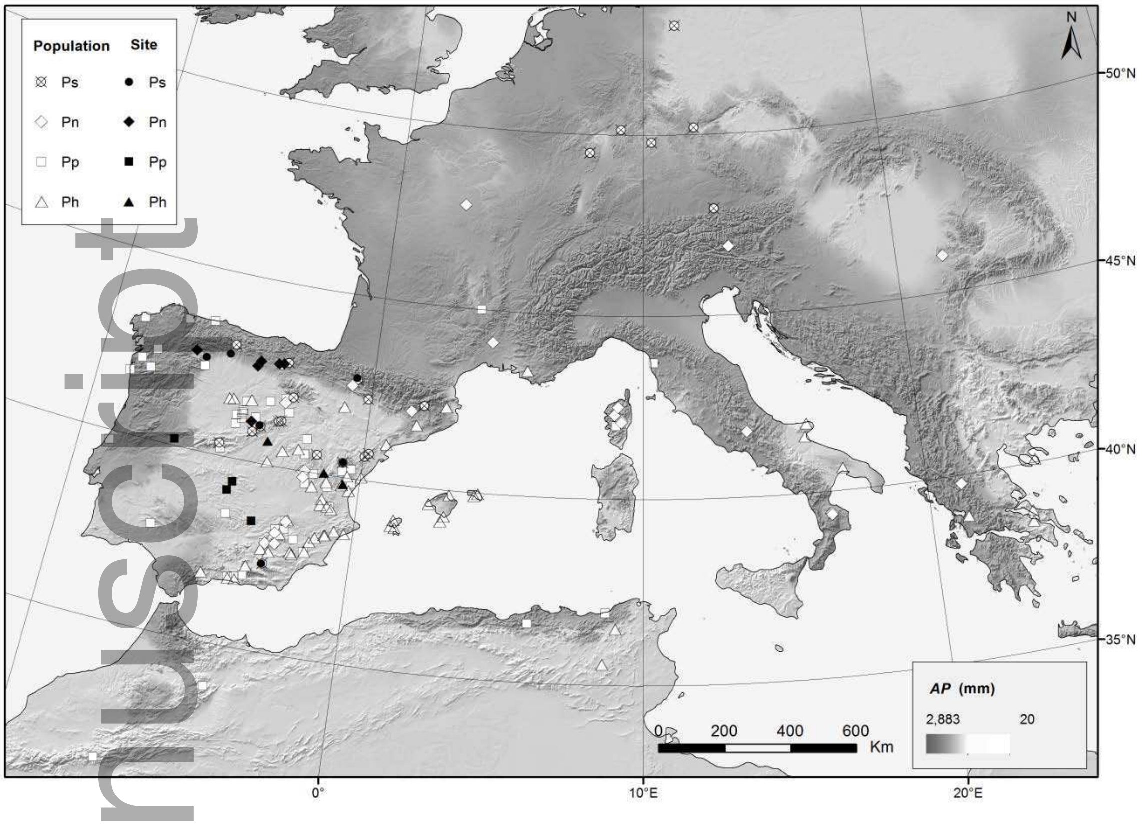

Figure 1. Location of common gardens (**Site**, filled symbols), and population origin (**Population**, unfilled symbols). Each pine species is represented by a different code and symbol: *P*. sylvestris (**Ps**, circle); *P*. *nigra* (**Pn**, star): *P*. *pinaster (***Pp**, square), and *P*. *halepensis* (**Ph**, triangle).

Model	**Hyperparameter**	**Model**	**Parameter**	**Insights from parameter**
Scaling Coefficient $\ln(a_{p_{(i)},s_{(i)}})$	μ_1 *Hierarchy*: Species***** *Meaning*: -allometric curve's intercept at average growing conditions.	Scaling Coefficient $\ln(a_{p_{(i)},s_{(i)}})$	α_{1p} *Hierarchy*: Population *Meaning*: -allometric curve's intercept at average growing conditions.	-assessing genetic differences among populations on their basal height. $\alpha_{1p} = \alpha_{1p_A} - \alpha_{1p_B}$ €, A and B are any two populations -quantify % of genetic differences based in € -quantify the range of genetic variation, sd(α_{1p}) -assessing adaptive values resulting from past demography of the species (gene pools allows for testing neutral patterns). One-way ANOVA -assessing adaptive values resulting from climatic or geographical clines due to local adaptation. Pearson correlations (ρ)
Scaling Coefficient $\ln(a_{p_{(i)},s_{(i)}})$	μ_2 *Hierarchy*: Species***** *Meaning*: -responsiveness of a species to low temperatures where it grows	Scaling Coefficient $\ln(a_{p_{(i)},s_{(i)}})$	α_{2p} *Hierarchy*: Population *Meaning*: -responsiveness of each population to low temperatures where they grow	-assessing genetic differences among populations on their response to temperature. $\alpha_{2p} = \alpha_{2p_A} - \alpha_{2p_B}$ €, A and B are any two populations -quantify % of genetic differences based in € -quantify the range of genetic variation, sd(α_{2p}) -assessing adaptive values resulting from past demography of the species (gene pools allows for testing neutral patterns). One-way ANOVA -assessing adaptive values resulting from climatic or geographical clines due to local adaptation in plastic responses to temperature. Pearson correlations (ρ)
Scaling Coefficient $\ln(a_{p_{(i)},s_{(i)}})$	μ_3 *Hierarchy:* Species***** *Meaning*: -responsiveness of	Scaling Coefficient $\ln(a_{p_{(i)},s_{(i)}})$	α_{3p} *Hierarchy:* Population *Meaning*: -responsiveness of	-assessing genetic differences among populations on their response to precipitation $\alpha_{3p} = \alpha_{3p_A} - \alpha_{3p_B}$ €, A and B are any two populations -quantify genetic differences % based in € -quantify range of genetic variation, sd(α_{3p}) -assessing adaptive values resulting from past demography of the species (gene pools allows for testing neutral patterns). One-way ANOVA -assessing adaptive values resulting from

Model	Hyperparameter	Model	Parameter	Insights from parameter
	a species to annual precipitation where it grows		each population to precipitation where they grow	climatic or geographical clines due to local adaptation in plastic responses to precipitation. Pearson correlations (ρ)

Model	Parameter	Insights from parameter
Scaling exponent $c_{p_{(i)}}$	β_1 *Hierarchy*: Species***** *Meaning*: -intercept of $c_{p(i)}$ on average conditions on diameter¿?	
Scaling exponent $c_{p_{(i)}}$	β_2 *Hierarchy*: Species***** *Meaning*: -responsiveness of the species to latitude	-if statistically significant, assessing the existence of a latitudinal cline This will suggest the existence of populations' adaptation to their local environment.
Scaling exponent $c_{p_{(i)}}$	β_3 *Hierarchy*: Species***** *Meaning*: -responsiveness of the species to altitude	-if statistically significant, assessing the existence of an altitudinal cline. This will suggest the existence of populations' adaptation to their local environment.

*****In this study, the species term is approximated as the average response from the set of populations assessed.

Figure 2. Summary information of the estimated parameters, hyperparameters and parameters, in the final tree height-diameter allometry model. We have described each one attending to its hierarchy, its significance and the set of research questions that can be addressed.