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One model to rule them all: A nationwide height–diameter model for 91 Spanish forest species

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ABSTRACT

Accurately characterizing tree allometry is essential for sustainable forest management to predict forest growth and yield, monitor long-term stand dynamics and assess the impacts of disturbances. Among different allometric attributes, past studies have focused on understanding the relationships between tree height and diameter at breast height (dbh), also known as height–diameter (h–d) relationships. Both variables are commonly used to estimate and predict tree and stand metrics (e.g., total volume, biomass and carbon) as well as to assess site productivity. Under limited budget and time constraints, h–d models, which predict tree heights using dbh measurements, provide a practical and cost-effective alternative. In this study, a mixed-effects h–d model was developed for making species-specific predictions for 91 tree species across broad geographic areas in Spain. A total of 1,512,721 observations were collected from the Spanish National Forest Inventory sample plots for analysis.

Results indicate that the final model, selected from a pool of 95 candidates, provides unbiased predictions of total tree height based on the 95% confidence interval of mean bias. In addition to dbh, the inclusion of site qualitative variables (stand origin, species mixture and biogeographic region) in the model plays an important role in improving the model predictability. For a given tree dbh, trees in plantations and pure stands tend to achieve greater heights than those in natural and mixed stands. Regional variation is species-dependent, while the Alpine region with a higher wind speed and cooler temperature tends to exhibit shorter trees compared to other regions. The proposed models are simple in structure and rely on easily-obtainable predictors, making them useful for field application and minimizing the need for complex measurements. This study provides an alternative quantitative tool for forest practitioners and managers when predicting total tree heights for diverse forest ecosystems across a wide range of geographic regions.

1. Introduction

Accurately characterizing tree allometry has been widely studied in forest management, ecology and modeling in order to predict forest growth and yield (Bravo et al., 2012), monitor long-term stand dynamics (Pretzsch, 2009) and assess the impacts of disturbances (e.g., wind and snow (Díaz-Yáñez et al., 2017) or hurricanes (Yang et al., 2022)). Tree allometry is driven by different biotic and abiotic factors (e.g., species composition, environment, disturbances) (Babst et al., 2013). For instance, increased competition stimulates height growth to guarantee light access, resulting in taller and more slender trees regardless of environmental conditions, as observed among several species and locations like ponderosa pine stands in the western United States (Qiu et al., 2021). Additionally, competition also influences crown architecture, as reported in boreal stands (Thorpe et al., 2010). Both intra- and interspecific competition have effects on tree allometry (Rodríguez De Prado et al., 2022), helping to disentangle species mixture effects. In addition, climate influences this relationship depending on local conditions and the ongoing effects of climate change (Rodríguez De Prado et al., 2022; Trasobares et al., 2022), supporting the understanding of its impact on tree allometry. As an example, Yang et al. (2022) reported that topographic and climatic variables are important in characterizing tree allometric relationships for Caribbean trees.

Among different allometric attributes, understanding the relationship between tree height and diameter at breast height (h–d) is vital, as both h and dbh are key variables for estimating and predicting tree and stand metrics (e.g., total volume, biomass, and carbon), as well as assessing site productivity (Pretzsch et al., 2015; Moreno-Fernández

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et al., 2018). However, obtaining accurate height measurements is often labor-intensive, time-consuming, and requires specialized expertise (Calama and Montero, 2004; Diéguez-Aranda et al., 2005; Yang and Burkhart, 2020). The h–d models allow tree height estimation from easily recorded dbh data, significantly reducing the cost and effort invested in forest inventories. As already mentioned, h records are particularly valuable for predicting essential forest metrics, such as tree biomass and carbon content, which typically requires both h and dbh as input variables (Ruiz-Peinado et al., 2012, 2011; Montero, 2005). Likewise, estimating tree volume commonly relies on both h and dbh as predictive variables (Blanco and Blanco, 2021; Diéguez-Aranda et al., 2009). Additionally, h records play a crucial role in predicting non-timber products, such as cone production in stone pine (*Pinus pinea*) forests (Calama et al., 2011) and cork yield in cork oak (*Quercus suber*) forests (Sánchez-González et al., 2008). To achieve this purpose, h–d relationships can facilitate the estimation of these variables by allowing h records to be obtained with reduced effort.

In the recent decades in Spain, forested areas have been expanding rapidly and cover 55% of the national territory (IEPNB, 2022). The increase in forest cover enhances the provision of various ecosystem services, including biodiversity conservation (Garrote et al., 2020), soil conservation, particularly in drought regions (Segura et al., 2021; Fernández-Ondoño et al., 2010), timber (Infante-Amate et al., 2022), and non-timber products such as mushrooms (Bonet et al., 2014). Additionally, forests play a crucial role in carbon sequestration (Bravo-Oviedo et al., 2021), which has gained increasing attention as a strategy to mitigate climate change through sustainable management (Ruiz-Peinado et al., 2017).

To ensure resilience and adaptability in Spanish forests, flexible and effective silvicultural strategies are required (Vadell et al., 2022; Bravo, 2022). In this context, mixed-species and uneven-aged stands have been promoted as they offer greater resistance and resilience compared to even-aged pure forests (Rodriguez de Prado et al., 2023; Muñoz-Gálvez et al., 2021; Vadell et al., 2022). However, implementing these strategies effectively requires reliable forest models, including h–d models, to support decision-making in stand dynamics, growth projections, and timber estimation (e.g., Bravo et al., 2012, 2025).

Given the heterogeneity of Spanish forests, h–d models have been developed for different species and regions across the country (Bravo et al., 2012), typically covering specific local areas and stand properties for a given species. For instance, different h–d models have been developed for *Pinus sylvestris* in the Atlantic (Diéguez-Aranda et al., 2005) and Mediterranean regions (Lizarralde, 2008) pure stands, while a separate model was developed for mixed stands with different parameterization depending on species composition (Rodríguez De Prado et al., 2022). Despite these efforts, gaps remain, and several species and regions are still not covered by existing models (see the compilation of h–d models for Spain in Appendix A).

Furthermore, while several existing models enhance the understanding of ecological effects on h–d relationships, their usability may be limited due to input requirements. For instance, some models require information such as soil water-holding capacity, which may be challenging and costly to obtain (Trasobares et al., 2022). Others rely on dominant height as an input variable (Gómez-García, 2013; Sánchez-González et al., 2007; Adame et al., 2008), potentially making both tree height and stand dominant height inestimable.

Therefore, the main objective of this study was to compare the variation in h–d relationships of Spanish tree species among different biogeographic regions, stand origins and species composition. Specifically, a mixed effects model was constructed using dbh and site variables as predictors and with species as a random effect, which provides species-specific predictions of total tree height by accounting for site conditions. The base form of the final model was selected from a list of 95 published h–d models in the literature. Data used in this study were queried from the second, third and fourth editions of the Spanish Forest National Inventory (SFNI), which includes more than one million curated observations from 91 tree species across the entire country of Spain (Alberdi et al., 2017). Although h–d modeling is not a novel research field, it remains a fundamental component in forest simulation and growth modeling frameworks. The strength of the model developed in this study relies on its usability, as it provides reliable height estimates based solely on readily available information (species identity, dbh, and basic stand descriptors), without requiring additional field measurements or specialized inventory inputs. The findings of this study not only offer insights into tree allometric relationships under varying site conditions but also deliver a practical, broadly applicable tool for forest managers and practitioners working across diverse ecosystems.

The findings of this study will not only offer insights into tree allometric relationships under varying site conditions but also provide a quantitative tool for forest managers and practitioners for predicting total tree height in diverse ecosystems.

2. Materials and methods

2.1. Data

In this study, the measurements used were collected from the Spanish National Forest Inventory (SNFI), specifically from the second (1986–1996), third (1997–2007), and fourth editions (ongoing since 2008), while data from the first edition (1965–1975) were excluded due to discrepancies in the experimental design and lower-quality tree height records. The SNFI follows a systematic design with a grid size of 1 km^2 for plot allocation. Each plot consists of four concentric circular subplots with radii of 5, 10, 15, and 25 m, where trees with a diameter at breast height (dbh) greater than 7.5, 12.5, 22.5, and 42.5 cm, respectively, were measured. Multiple tree-level and plot-level variables were recorded, along with information on regeneration, scrubland, soil properties, and other aspects, although these were not used in our study. Sample plots were distributed across the entire country, covering the four biogeographic regions of Spain (Atlantic, Mediterranean, Alpine, and Macaronesian) (MITECO, 2024) as shown in Fig. 1, and encompassing various stand conditions, species, and management guidelines.

2.1.1. Biogeographic region

Climate variability across the study area was considered through the classification of biogeographic regions. Although a more detailed classification could be used, this classification was considered to easily promote the usability of the final model. Biogeographic regions include four different areas and it relies on the climate, geology, soil characterization, and topography information of the whole country, used as a basis to spatially classify the Spanish territory (Galicia et al., 2014). Fig. 1 offers a visual classification of each SFNI plot location used in our study across the biogeographic region limits.

The Mediterranean region, covering most of Spain, is characterized by dry and warm summers and wet, cool winters. It includes both mountainous and flat areas and is the most representative climatic region of Spain (Sundseth, 2010d). The Atlantic region, located in the northern part of the country, extends across most of Europe's northern coastal areas (Sundseth, 2010b). It is a mountainous region where summer droughts are less intense, and annual rainfall is higher due to the proximity of the sea, which moderates daily and annual climate variability and extends the growing season. The Alpine region, covering the Pyrenees in the northeast of Spain, is characterized by steep mountains and a relatively cold, arid climate, which limits forest species' growth and establishment (Sundseth, 2010a). Lastly, the Macaronesian region includes the Canary Islands, located off the west coast of Africa and surrounded by the Atlantic Ocean. Its warm climate throughout the year and unique location allow the presence of species not found in other regions of Spain or Europe, making it exceptionally rich in terms of biodiversity (Sundseth, 2010c).

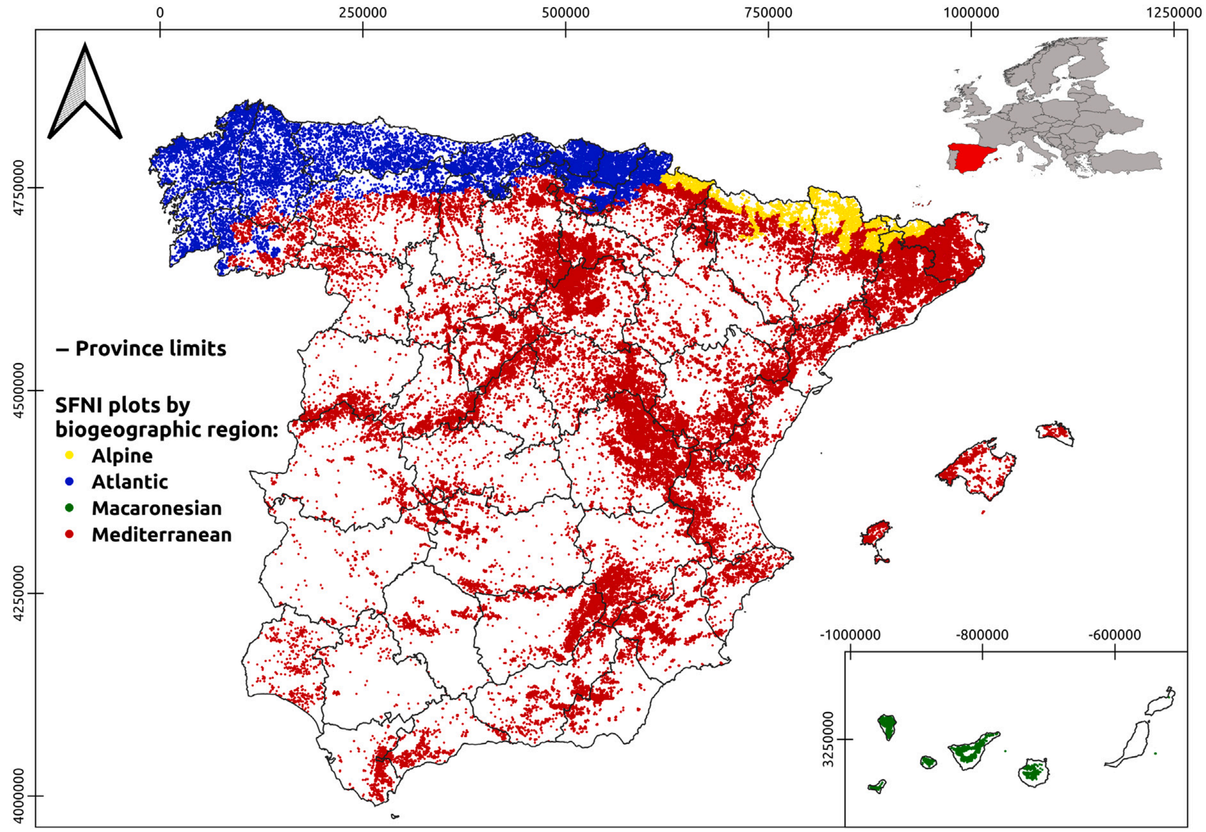


Fig. 1. SFNI plots distribution. The color of each plot, represented by a dot, refers to the biogeographical region where it is located. Notice that the Canary Islands were moved to zoom in on the map content. Coordinates are shown in the ETRS89-30N system.

2.1.2. *Stand origin and species mixture*

In a given region, plots were further divided into four groups based on stand origin (natural or artificial forest) and species mixture (pure or mixed-species forest). Stand origin information was obtained from the labels in the original dataset, with plots lacking this information excluded from the analysis.

Pure and mixed-species forests were classified based on the number of species and the proportion of each species within a population. This classification has been discussed from a European perspective, aiming to integrate the distinct characteristics of different European stands (Bravo-Oviedo et al., 2014). In this study, a plot is defined as a mixed stand if the combined proportion of at least two species exceeds 90% of the total basal area per hectare, and the proportion of either species is over 15%. This approach aligns with the previously mentioned classification and has been applied in prior studies on Iberian Peninsula stands (Rodriguez de Prado et al., 2023; Rodríguez De Prado et al., 2022).

2.1.3. *Tree data*

For each tree, its size (dbh and height), stem shape (straight, bent, forked, etc.), position, and damages (biotic and/or abiotic) were recorded in the original database (Alberdi et al., 2017). Given the high variability in the original dataset, only healthy trees without special conditions were included in the study to avoid bias in the allometric relationships. During data curation, observations were removed if (1) the recorded h–d relationship exhibited extreme values that could result from misclassified damage (e.g., an unrecorded broken top), (2) specific tree characteristics could alter the general trend of the h–d relationships, including non-straight shapes (e.g., forked, twisted), biotic or abiotic perturbations (e.g., illness, dead trees), and specific situations like debarked (*Quercus suber*) or resin-tapped (*Pinus pinaster*) trees which effects on tree allometry are unknown, (3) plot coordinates were misrecorded, as it was not possible to assign a climate region on the following analysis, or (4) species representation after the previous filters was too low, leading to the exclusion of certain trees to avoid deviations. From the initial dataset of 3,373,698 trees at the time of acquisition (SFNI4 not yet completed), a total of 1,512,721 h–d pairs were used in our study after data curation, covering 91 species. The summary statistics of observations in each combination are given in Table 1.

2.2. *Statistical methods*

To quantify the variation in h–d relationships, the statistical analysis in this study followed three main steps. First, we included 95 h–d models from the literature as base models and selected the top five candidates based on goodness-of-fit metrics. In the second step, these candidate models were used to build nonlinear mixed-effects models, incorporating species as a random effect and stand origin, species mixture, and biogeographic region as fixed effects. Finally, to account for repeated tree measurements, a cluster bootstrap analysis was conducted to provide statistical insights into model performance.

Data processing and statistical analysis were performed in R version 4.1.2 (R Core Team, 2021). Detailed descriptions of the statistical procedure are given below.

2.2.1. *Step 1: Selection of model candidates*

Aiming to model the h–d relationship of 91 species using a unified approach, we evaluated 95 base h–d models. Although only a few of these models have been applied in Spain (see Appendix A), most have been widely used in other regions such as Europe (e.g., Lebedev, 2020; Lebedev and Kuzmichev, 2020), North America (e.g., Moore et al., 1996; Temesgen et al., 2007; Temesgen and v. Gadow, 2004), and other parts of the world (e.g., El Mamoun et al., 2013; Wagle

Table 1
Summary of tree dbh (cm) and total height (m) by biogeographic region, stand origin and species mixture. Both tree variables are summarized by the minimum (min), maximum (max), mean (mean) and standard deviation (sd).

Biogeographic region	Stand origin	Species mixture	dbh mean	dbh sd	dbh min	dbh max	h mean	h sd	h min	h max
Alpine	Artificial	Mixed	20.49	6.97	7.50	46.75	10.99	3.79	3.50	22.50
		Pure	20.89	7.43	7.50	62.70	12.03	4.87	3.00	31.00
	Natural	Mixed	27.36	13.26	7.50	117.10	13.94	5.23	2.50	39.50
		Pure	27.21	12.04	7.50	130.50	13.78	5.27	1.00	41.50
Atlantic	Artificial	Mixed	26.93	13.34	7.50	106.30	18.03	7.15	2.50	59.10
		Pure	27.94	13.13	6.85	118.70	19.08	7.57	2.00	54.20
	Natural	Mixed	29.97	15.51	7.50	143.90	16.78	5.96	3.00	52.00
		Pure	30.54	15.21	7.30	137.00	16.97	6.11	2.50	49.60
Macaronesian	Artificial	Mixed	34.33	13.78	8.00	91.70	17.08	6.28	4.00	39.90
		Pure	28.30	10.86	7.55	85.30	15.94	5.92	2.90	34.20
	Natural	Mixed	32.87	19.31	7.50	123.20	16.14	6.06	3.00	37.30
		Pure	35.18	17.15	6.70	178.20	15.91	6.15	2.50	50.50
Mediterranean	Artificial	Mixed	20.93	8.63	7.20	130.50	10.80	4.41	2.50	41.80
		Pure	21.35	8.08	7.50	108.50	11.63	5.38	2.20	47.00
	Natural	Mixed	25.24	11.97	7.50	140.00	11.81	4.49	2.00	43.10
		Pure	25.37	11.65	6.75	174.00	11.94	4.60	1.50	44.20

et al., 2024; Scaranello et al., 2012), including all of them to identify the most accurate representation across the various species and stand conditions examined. All the base models were extracted from the scientific literature, using dbh as the only predictor variable, and can be consulted in the attached data availability. All 95 models were fitted for each species separately using the nlsLM function in the minpack.lm package (Elzhov et al., 2023), assigning three different initial starting parameter combinations as maximum trials for model convergence. Models that failed to converge in parameter estimation for any species were excluded for further analysis. Model performance was compared using the Akaike Information Criterion (AIC) (Akaike, 1998). For a given species, models were ranked based on the minimum AIC values. The selection frequency of each model as the best was calculated, and the five most frequently chosen models were selected as candidates for the next step. Additionally, the final fitted parameter values among species were averaged and used as starting parameter values for the next step.

2.2.2. *Step 2: Nonlinear mixed models*

After the top five base models were selected, nonlinear mixed models were built using each base equation as the underlying model. Species were included as a random effect, while three stand variables, including stand origin (natural or artificial), species mixture (pure or mixed stand), and biogeographical region (Mediterranean, Atlantic, Alpine, or Macaronesian), were incorporated as fixed effects. Model fitting was conducted using the nlme R package (Pinheiro et al., 2017). For each selected base model, all possible combinations of random and fixed effects were tested. Models that successfully converged were ranked using AIC scores, with the best model and fixed effects combination identified based on the minimum AIC value.

2.2.3. *Step 3: Final model evaluation*

Since the dataset included three editions of the same inventory, some trees had two or even three repeated measurements. To account for this, a cluster bootstrap analysis was performed. Cluster bootstrapping is a nonparametric resampling procedure commonly used in parameter estimation for grouped or multi-level data, which accounts for the repeated measurements for trees (e.g., Field and Welsh, 2007; Davison and Hinkley, 1997). In cluster bootstrapping, observations are selected in groups to retain the correlation structure within each group. In this study, individual trees were treated as groups and randomly selected with replacement. All measurements from the selected trees were used for model fitting. This process was repeated 1000 times (i.e., 1000 bootstrap samples), estimating mean bias (MB) and root mean squared error (RMSE) in each iteration.

3. Results

3.1. *Model selection*

The top 5 h–d base models were selected from a pool of 95 candidate models based on their AIC values and the frequency of their selection across studied species. Additionally, the models were required to fit all the studied species to ensure a high likelihood of convergence in the following steps. Table 2 presents the selected model equations along with the number of times they were selected and their ranking position. Some discarded candidates provided optimal solutions for individual species among the base models studied. However, they were excluded when they failed to fit for other species or were selected as the best model less frequently. While the five selected base models have two parameters (a and b), several discarded models featured more complex structures, incorporating two to four parameters.

Using the top five selected models, all possible combinations of random and fixed effects were tested and ranked based on AIC. The best version of each model, along with its AIC values, is summarized in Table 3. The five studied base models reached similar performance levels with their optimal combinations of random and fixed effects. Model M4 was the best-performing model based on our results, with its final parameters, along with species-specific and fixed-effect parameter adjustments, provided in Appendix B.

Although not shown in the table, alternative configurations for the M4 model yielded higher performance values than the best alternatives for other candidate models. In all the top models presented, both the a and b base parameters were modified by species as a random effect. Among them, models M4, M3 and M5 reached their highest performance when all three stand variables, included as fixed effects, affected both parameters. In contrast, the M2 and M1 models excluded stand origin as an effect on the b and a parameters, respectively.

3.2. *Prediction accuracy*

To assess the final model's performance and account for repeated measurements in the dataset, a cluster bootstrap analysis was conducted using 1000 bootstrap samples. Mean bias (MB) and root mean squared error (RMSE) of predictions were calculated to assess the variability and systematic error in model predictions. According to the 95% confidence interval (MB: −5.764 m – 6.773 m with a median of −0.223 m), the final model can provide unbiased predictions of total tree heights. The 95% confidence interval of RMSE ranges from 3.110 m to 3.117 m with a median of 3.114 m. As shown in Fig. 2(f), the pairs of the predicted and observed total tree heights scatter evenly along a diagonal line, which confirms that the total tree height can be reliably predicted by the final model.

Table 2
Top five candidate h–d base models selected from 95 candidates. The table includes the model name, equation, the number of times each model was selected as the best for a given species (*N best*), and its ranking based on selection frequency. Some models were excluded because they did not fit all species included in the study.

Model name	Original equation	N best	Average rank	Reference
M1	$h = a + b \cdot \log(\mathrm{dbh})$	9	1	Scaranello et al. (2012)
M2	$h = \frac{a \cdot \mathrm{dbh}}{(b + \mathrm{dbh})}$	7	2	Scaranello et al. (2012)
M3	$h = 1.3 + \frac{a \cdot \mathrm{dbh}}{(b + \mathrm{dbh})}$	6	3	El Mamoun et al. (2013)
M4	$h = 1.3 + a \cdot (\log(1 + \mathrm{dbh}))^b$	5	5	El Mamoun et al. (2013)
M5	$h = 1.3 + \frac{\mathrm{dbh}^2}{(a + b \cdot \mathrm{dbh})^2}$	4	7	El Mamoun et al. (2013)

The final parameter estimates for the model and their variability across the 1000 cluster analyses were also examined (Table 4). Smooth variations were observed for each parameter β_a and β_b, as well as their adjustments based on fixed-effect covariates. Among them, the Macaronesian biogeographical region exhibited the highest variability.

3.3. Variation of h–d relationships among species

Species variability was accounted for through the model's random effect, with species-specific parameter adjustments detailed in Appendix B, Table B1. Fig. 2 compares observed and predicted tree heights for some of the species studied, highlighting differences in the h–d relationship across tree shapes and data availability. The results indicate lower predictive accuracy for taller trees in cases (a) and (b) (*Pinus sylvestris* and *Quercus petraea*), as deviations from the red reference line increase with height. In contrast, cases (c), (d), and (e) (*Eucalyptus globulus*, *Cupressus arizonica*, and *Populus x canadensis*, respectively) show closer alignment between predicted and observed values across the full range of tree heights, suggesting better model performance for these species. Case (f) aggregates all trees included in the study, illustrating the full range of height variability, from 1.0 to 59.1 m, and the overall predictive behavior of the model across all species.

3.4. Variation of h–d relationships among stand origins, species mixtures and biogeographic regions

Stand variability was accounted for through the model's fixed effect, considering stand origin, species mixture and biogeographic region parameter adjustments (see Appendix B, Table B2). Fig. 3 illustrates the predicted h–d relationships for selected species under different stand characteristics included in the model. While fixed effect coefficients are common for all the species studied, representative case studied were selected for each stand variable. Case (a) focuses on *Populus alba* trees growing in natural stands and plantations, where taller trees are predicted in plantations for the same dbh. Case (b) examines *Quercus robur* trees in pure and mixed stands, with taller trees predicted in pure stands compared to mixed ones. Case (c) depicts *Pinus pinaster* trees across four biogeographical regions, considering Alpine, Atlantic, Macaronesian, and Mediterranean. Results reveal regional differences, highlighting the Atlantic region as the one producing the tallest trees for a given dbh.

While the developed model accounts for all possible combinations of stand origin, stand mixture, and biogeographical region for each species, the graphs isolate specific comparisons to facilitate interpretation. Although the adjustment parameters apply to all studied species, some species-biogeographical region combinations may be absent from the original dataset due to natural condition incompatibilities.

4. Discussion

This study introduces a new height–diameter model parameterized for 91 of the most common forest species in Spain under different stand conditions, addressing a significant gap in this modeling field. While site-specific, calibrated models can provide higher predictive, they are often unavailable for many regions and species. Our models serve as a practical baseline, offering reliable predictions across diverse stand conditions with minimal data requirements.

4.1. Model suitability as baseline for tree height predictions

Due to the choices made regarding the variables used, the primary strength of our model lies in its usability. Since it requires only basic tree data (species and dbh) and qualitative stand information (stand origin, species mixture, and biogeographical region), they are well-suited for situations where comprehensive inventory data is limited. For example, this model provides useful predictions without requiring plot installation or extensive stand measurements. Although adding site-specific variables could improve accuracy by making the model more precise, it would also increase data demands and the associated inventory effort, limiting their applicability in data-scarce contexts.

In terms of modeling, while previous studies have used various stand variables to predict tree height (see Cañadas et al. (1999) and studies summarized in Appendix A), we opted to include only tree dbh as a predictive variable in the baseline models for simplicity. After analyzing 95 equations from the literature, the top five h–d models selected as baseline demonstrated comparable performance metrics, confirming their suitability for our study. This step revealed that different models performed optimally for different species, highlighting the need for further refinement in developing species-specific h–d models to enhance predictability in future research. Furthermore, the top five models chosen based on AIC included only two parameters in their equations. This underscores the impact of AIC in promoting model simplicity, which in turn reduces computational demands in subsequent analyses, particularly when fitting non-linear mixed effect models with various combinations of random and fixed effects as in our case.

Previous studies have shown that simplifying models to predict forest metrics like productivity (Rodríguez et al., 2010) or volume (Marziliano et al., 2018) does not compromise estimation accuracy. In our study, the design of the initial dataset shaped the challenges and opportunities encountered. While the dataset included extensive data from diverse regions and species, enhancing its applicability across various scenarios, the inventory plot design presented some difficulties. Organized as concentric circular plots with size-based tree recording criteria, this structure may introduce biases in stand or competition variables due to varying tree expansion factors across circles. To avoid such biases, we excluded quantitative stand variables commonly used like stand density or basal area. We also have decided to omit dominant height, a variable often used for its predictive power on tree height (Rodríguez De Prado et al., 2022; Rodríguez-Puerta et al., 2023), but prone to creating dependencies between independent and dependent variables in the case of tree height estimation. Instead, we decided to include the already mentioned stand qualitative variables. We also tested alternative variables related to stand structure, such as the ratio between tree dbh and stand quadratic mean diameter (dbh/dg) and the ratio of tree basal area to stand basal area (g/G). These variables serve as proxies for the social status of the tree within the stand, but model predictability did not increase enough to justify its inclusion.

Beyond the model variables simplicity, the methodological approach aligned with the main objective of the study. Selecting a single model form reduces complexity on its application, while its parameterization for different species and stand characteristics allows to cover a broader range of situations. Additionally, the proposed methodology provides a practical framework for application in other national-level studies using their respective National Forest Inventories

Table 3

Summary of the top-performing models selected based on lowest AIC values. In the equations, β represents each parameter, a and b. The base forms, β_a and β_b, correspond to the parameters estimated for the entire dataset. Subscripts indicate the random and fixed-effect covariates included in the model: *0* refers to species (x_0, random effect), and *1* to *3* refer to fixed effects (stand origin (x_1), species mixture (x_2), and biogeographical region (x_3)), which are incorporated through dummy variables. Models were ranked based on AIC, with lower values indicating better performance. The best-performing model is shown in bold.

Model name	Equation	AIC
M4	$h = 1.3 + (\beta_a + \beta_{0a} * x_0 + \beta_{1a} * x_1 + \beta_{2a} * x_2 + \beta_{3a} * x_3) \cdot (\log(1 + \text{dbh}))^{(\beta_b + \beta_{0b} * x_0 + \beta_{1b} * x_1 + \beta_{2b} * x_2 + \beta_{3b} * x_3)}$	**7734375.17**
M2	$h = \dfrac{(\beta_a + \beta_{0a} * x_0 + \beta_{1a} * x_1 + \beta_{2a} * x_2 + \beta_{3a} * x_3) \cdot \text{dbh}}{((\beta_b + \beta_{0b} * x_0 + \beta_{2b} * x_2 + \beta_{3b} * x_3) + \text{dbh})}$	7753403.79
M3	$h = 1.3 + \dfrac{(\beta_a + \beta_{0a} * x_0 + \beta_{1a} * x_1 + \beta_{2a} * x_2 + \beta_{3a} * x_3) \cdot \text{dbh}}{((\beta_b + \beta_{0b} * x_0 + \beta_{1b} * x_1 + \beta_{2b} * x_2 + \beta_{3b} * x_3) + \text{dbh})}$	7756898.38
M5	$h = 1.3 + \dfrac{\text{dbh}^2}{((\beta_a + \beta_{0a} * x_0 + \beta_{1a} * x_1 + \beta_{2a} * x_2 + \beta_{3a} * x_3) + (\beta_b + \beta_{0b} * x_0 + \beta_{1b} * x_1 + \beta_{2b} * x_2 + \beta_{3b} * x_3) \cdot \text{dbh})^2}$	7757645.11
M1	$h = (\beta_a + \beta_{0a} * x_0 + \beta_{2a} * x_2 + \beta_{3a} * x_3) + (\beta_b + \beta_{0b} * x_0 + \beta_{1b} * x_1 + \beta_{2b} * x_2 + \beta_{3b} * x_3) \cdot \log(\text{dbh})$	7768132.02

Table 4

Final model parameters (β_a and β_b) and their variability based on the cluster bootstrap analysis. The 0.5 quantile (median), representing the final parameter value, is shown, with the 0.025 and 0.975 quantiles presented in brackets. Parameter standard deviation (σ) and adjustments based on species mixture (*Mixed*), stand origin (*Plantation*), and biogeographical region (*Atlantic, Alpine, and Macaronesian*) are also detailed.

Parameter	Estimated	σ	Mixed	Plantation	Atlantic	Alpine	Macaronesian
a	1.392 (1.361/1.418)	0.672 (0.650/0.698)	0.018 (0.016/0.020)	−0.012 (−0.014/−0.010)	0.202 (0.198/0.205)	−0.032 (−0.037/−0.027)	0.184 (0.169/0.199)
b	1.990 (1.975/2.006)	0.360 (0.336/0.378)	−0.039 (−0.041/−0.037)	0.038 (0.036/0.041)	−0.069 (−0.072/−0.066)	0.035 (0.030/0.039)	−0.200 (−0.217/−0.182)

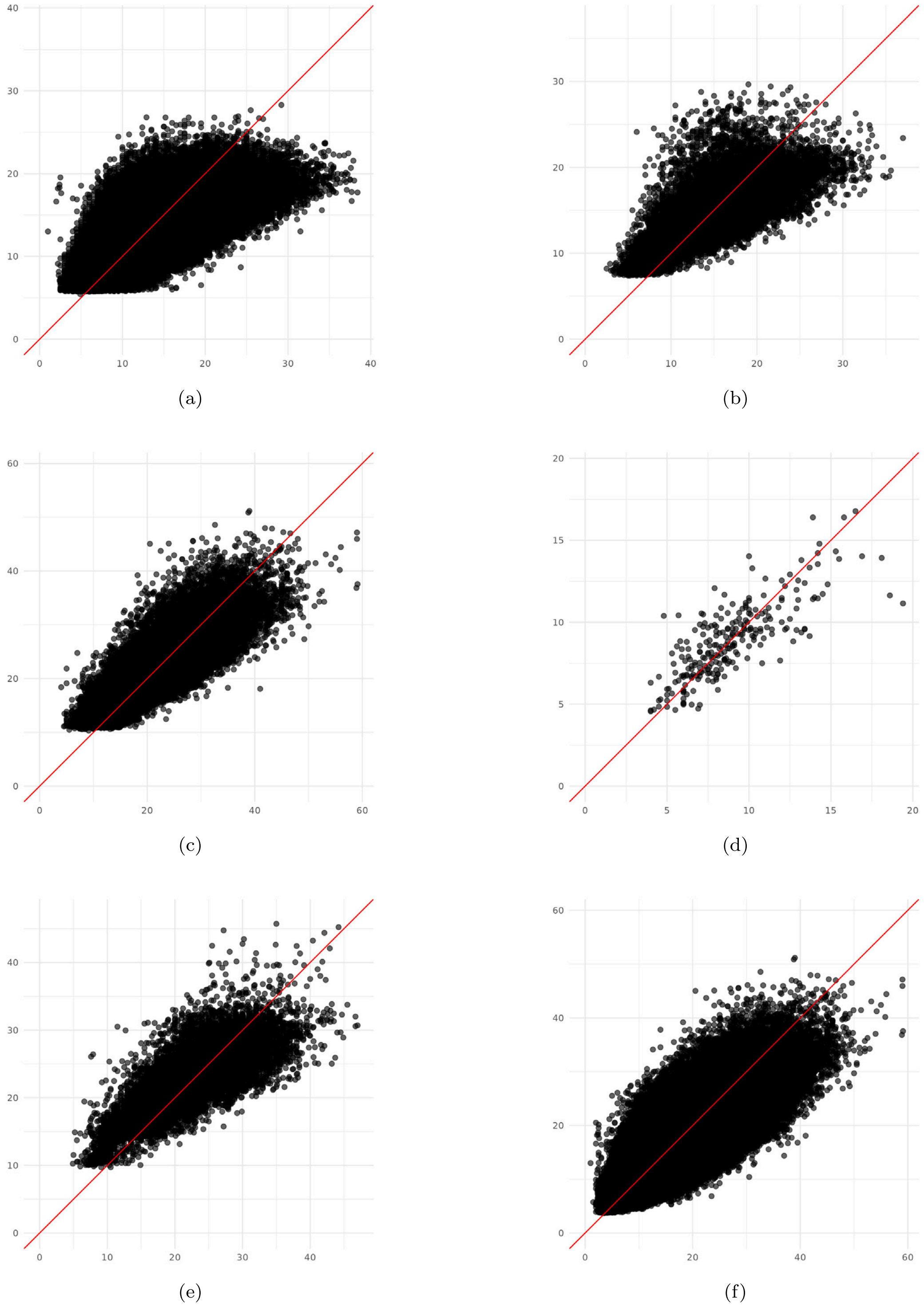
(NFIs). This establishes a baseline of user-friendly models for species and regions where no other models are available. Furthermore, this approach is adaptable for modeling other forest dynamics and static processes, making it valuable for addressing critical scenarios in forest management. NFIs have proven to be robust frameworks for developing decision-making tools that support forest management (Marcot et al., 2012; Andersson et al., 2009), enabling coverage of extensive areas that are otherwise challenging to address and providing a representative variety of stand characteristics.

To evaluate the model, the cluster bootstrap analysis accounted for the effect of repeated measurements in the initial dataset. RMSE values remained stable across the studied quantiles, suggesting that while bias is present mostly at extreme values, the model maintained a uniform error structure, reinforcing its reliability for most cases. The MB results indicate that the model exhibited minor overall bias in its predictions (−0.223 m) but showed substantial variation across the analyzed quantiles (−5.764 to 6.773 m for $Q_{0.025}$ and $Q_{0.975}$, respectively), suggesting that the model under- or overestimated tree height in certain cases with extremely deviation. Despite the wide bias range, this outcome was expected given the large sample size. Large deviations for specific individuals are common when studying the h–d relationships, even within a single tree species under standard conditions (Gómez-García et al., 2015; Gómez-García, 2013). These deviations are likely related to untracked tree characteristics, such as past damage or disease, which can alter allometry. In our study, we applied a common approach across species with different growth patterns (Babst et al., 2013; Yang et al., 2022), varying sensitivity to intra- and interspecific competition (Rodríguez De Prado et al., 2022; Riofrío et al., 2019), and differing responses to climate conditions (Trasobares et al., 2022), increasing the variability captured in the model. As a result, even when large biases can be returned under specific conditions, the model demonstrated good overall behavior.

4.2. Variability of height–diameter relationships among tree size, species and stand conditions

The final model exhibited varying performance depending on species and stand characteristics. In general, lower predictive accuracy was observed for taller trees in certain species able to reach huge dbh and/or height dimensions, such as *Pinus sylvestris* and *Quercus petraea*. Similar declines in predictive power have been noted in previous studies conducted in Spain (Calama and Montero, 2004; Sánchez-González et al., 2007). This limitation reflects a common challenge in modeling h–d relationships for over-mature trees, as these relationships often follow distinct trends depending on species and site conditions. It is worth noting that in Spain, mature or over-mature stand conditions are often reached at smaller tree heights compared to other European countries (Brandl et al., 2018). This is largely due to the generally lower site quality across many Spanish forest regions, particularly in Mediterranean and mountainous environments. As a result, the upper limit of height growth tends to occur at lower absolute values compared to more productive areas. Additionally, the scarcity of observations for extreme values further constrained the model's performance, making it unsuitable for such cases. To address this limitation, incorporating predictors such as site quality, climatic variables (Sánchez-González et al., 2007), or dominant height and dominant diameter (Crecente-Campo et al., 2010) can enhance model performance for taller trees. Calibration methods have also proven effective for improving predictive accuracy in these scenarios (Castedo-Dorado et al., 2006). Conversely, the model exhibited notable robustness when applied to species with limited data records, such as *Cupressus arizonica*, allowing for the parameterization of a total of 91 species. Although more species were present in the initial dataset, data curation reduced the number of records for some, leading to their exclusion from the analysis. Additionally, during the curation process, trees with specific characteristics (such as non-straight shapes, disease symptoms, resin-tapping, or bark removal) were also excluded, limiting the applicability of the model to trees not affected by these conditions.

The inclusion of stand qualitative variables in the model has played a significant role in improving predictability, as previously noted by other authors (López-Sánchez et al., 2003; Temesgen and v. Gadow, 2004; Li et al., 2015). Different model trends were observed between natural stands and plantations. In even-aged plantations, uniform spacing and controlled competition reduce variability in the h–d relationship, resulting in more consistent growth patterns among trees and enhancing model predictability (Buford and Burkhart, 1987; Li et al., 2015). In contrast, natural stands exhibit greater variability due to irregular spatial distribution of trees, diverse competition patterns (Mason et al., 2007), and higher species and age class diversity (Duan et al., 2018). Our findings indicate that, for a given dbh, trees in plantations tend to achieve greater heights, aligning with the management objectives of such stands, where taller trees are prioritized to maximize



(a)

(b)

(c)

(d)

(e)

(f)

Fig. 2. Comparison of observed (x-axis) and predicted (y-axis) tree heights (m) for single tree species with different amounts of data available and h–d trends. The red line indicates the 1:1 line. Species represented are: (a) *Pinus sylvestris*, 352,379 trees; (b) *Quercus petraea*, 16,674 trees; (c) *Eucalyptus globulus*, 36,271 trees; (d) *Cupressus arizonica*, 247 trees; (e) *Populus x canadensis*, 15,516 trees; (f) all studied species combined, 1,512,721 trees.

timber yields. On the other hand, the greater variability in size, spatial distribution, and age classes in natural stands fosters diverse growth strategies, where height growth is not necessarily a priority of the tree, thus justifying our results.

When analyzing species mixtures, pure stands were found to exhibit greater tree heights for a given dbh compared to mixed stands. This finding aligns with the previously mentioned factors of stand variability related to stand origin, as mixed forests introduce an additional layer of complexity due to the presence of multiple species. Prior studies comparing mixed and pure stands have highlighted differences in species growth responses within mixtures, reporting varying patterns depending on the species and their combinations (Pretzsch et al., 2015; Thurm and Pretzsch, 2016; Cattaneo et al., 2018; Riofrío et al., 2017). For instance, *Pinus sylvestris* demonstrated higher dbh and height in mixed stands compared to pure stands, whereas *Fagus sylvatica* exhibited smaller sizes in both dbh and height in mixed stands. Remarkably,

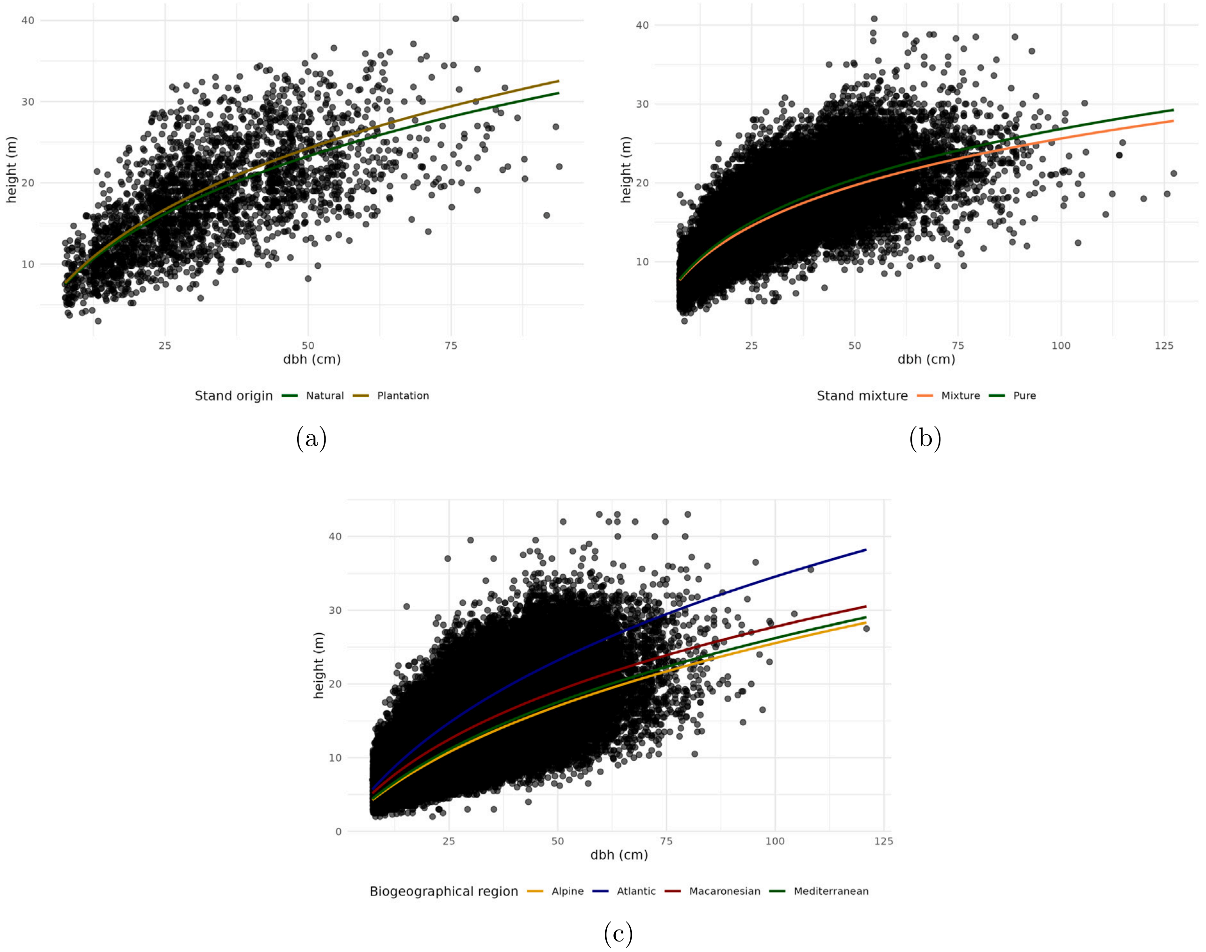


Fig. 3. Model prediction behavior using different species-specific and stand characteristic parameters. The graphs show tree dbh (x-axis) and height (y-axis) observed values for one species, while each line represents the model behavior associated with a specific stand characteristic, with default values for others. (a) *Populus alba* values (2627 trees) for each stand origin: natural (green) and plantation (brown). (b) *Quercus robur* values (26,948 trees) for each stand mixture: pure (green) and mixed (orange). (c) *Pinus pinaster* values (228,084 trees) for each climate region: Alpine (yellow), Atlantic (blue), Macaronesian (red), and Mediterranean (green).

the slenderness of *Pinus sylvestris* was reduced in mixed stands due to a greater increment in dbh relative to height, while *Fagus sylvatica* showed increased slenderness under similar conditions (Pretzsch et al., 2015). The complexity of these dynamics is further compounded by variations in shade tolerance (Tucker et al., 2024), which allow for the development of distinct height layers within mixed stands (Thurm and Pretzsch, 2016), affecting both stand structure and neighborhood competition. These differences in light utilization among species represent an intriguing area for future research, especially given the growing significance of mixed stands in contemporary and future forest management strategies in the context of climate change (Bravo, 2022; Pretzsch et al., 2017). Although stand structure (e.g., even-aged vs. uneven-aged) and dynamics such as shade tolerance and competition were not explicitly included in the model, they may underlie some of the effects observed for the species mixture and stand origin results in this study.

The biogeographic region emerged as a critical factor in explaining differences in h–d relationships among species across diverse environments as reported in previous studied (Huang et al., 2000). Our results revealed that the most pronounced differences in the Atlantic region, which is characterized by higher annual rainfall and greater productivity. Conversely, the Alpine region exhibited lower heights for a given dbh, likely driven by faster wind speed and cooler temperatures. A similar trend was observed in the Mediterranean region, where stress appears linked to summer drought limiting tree growth (Diego Galván et al., 2015). The Macaronesian region showed the second higher height values for a given dbh, while they were closer to the Mediterranean than the Atlantic ones. In those cases represented by fewer data records, model performance was not significantly compromised, as indicated by the model evaluation of parameter estimations. The biogeographic region classification can be understood in our model as a proxy of forest productivity. In this sense, a national-level analysis of five reference species revealed that *Pinus pinaster* subsp. *atlantica* exhibited higher productivity in the Atlantic region, with productivity declining at higher altitudes. Conversely, other species, such as *P. nigra* in the Mediterranean and Alpine regions and *P. sylvestris* in the Atlantic, Mediterranean, and Alpine regions, demonstrated the opposite trend (Moreno-Fernández et al., 2018). Additionally in a different study, species such as *P. radiata* showed greater sensitivity to soil fertility and lower productivity in areas with higher rainfall, potentially linked to steeper slopes (Romanyà and Vallejo, 2004).

Although environmental and climatic variables were not added in the models, the biogeographic region classification may help explain the variability observed. Further analyses by species could provide deeper insights into how regional climatic conditions influence h–d relationships, where soil implications can be interesting to address too. Additional descriptive variables related to forest management history may also influence model performance for specific species. For instance, the stand regime (high forest or coppice) could significantly affect h–d relationships in species with strong resprouting capacity, such as *Quercus pyrenaica*, where coppice and high forest management are quite different according to stand dynamics (Vázquez-Veloso et al., 2025; Crespo and García, 2013). In contrast, this variable may be less informative for other species included in the study. Other structural descriptors, such as stand structure (even-aged vs uneven-aged), stand maturity, or historical interventions, while not considered in this work, could also have species-specific effects on tree allometry and should be considered in future modeling species-specific studies.

4.3. Implications in forest management practices

Growth and yield models have been developed for different species and regions across Spain (Bravo et al., 2012), supporting forest management practices by estimating both current and future stand characteristics and yields. Among them, h–d models have been developed to reduce the effort associated with tree inventory. However, limitations have been identified in model usability, particularly regarding the acquisition of predictive variables (Trasobares et al., 2022), as well as model input and output dependencies that may restrict their applicability (Adame et al., 2008; Sánchez-González et al., 2007; Gómez-García, 2013). Additionally, several species and regions have not been addressed by existing models (see the compilation of h–d models for Spain in Appendix A), resulting in gaps that can compromise their usability. Considering these limitations and the boundaries of its application, our model can serve as a baseline in cases where species-specific local models are unavailable. Its simplicity, along with the wide range of species and stand characteristics covered, facilitates its adoption by forest managers and landowners. Furthermore, its use can reduce the effort required for field inventory, decreasing both the time and financial resources needed.

Furthermore, this model addresses existing gaps in simulation workflows. Variables such as timber biomass (Ruiz-Peinado et al., 2012, 2011) or volume (Lizarralde, 2008; Manrique González et al., 2017) rely on tree height as an input, but commonly this variable is not recorded in the field inventory for all of the trees. Using that model tree height can be estimated and then the remaining target variables estimated. Additionally, without accurate height values, the usability and accuracy of the aforementioned models are compromised.

To enhance accessibility, our h–d model was implemented in the SIMANFOR simulation platform (Bravo et al., 2025), simplifying the application of the correct model form and the selection of the proper parameterization for different case studies. Additionally, it has been made available in Excel, R, and Python, ensuring broader usability across different analytical environments (Appendix C).

5. Conclusion

Non-linear mixed-effect models have proven to be a powerful technique for addressing situations with unequal data availability across different tree species in forest biometrics. In this study, this approach was applied to the Spanish Forest National Inventory to develop height–diameter models for the most common Spanish forest species, with the initial goal of creating a single model capable of tracking diverse forest characteristics. To capture the allometric variability of each species, the model incorporated stand information, including stand origin, species mixture, and biogeographic region. The resulting model is a unified expression parameterized for 91 forest tree species across Spain. While locally calibrated models may outperform it in specific contexts, this model serves as a reliable baseline when no other alternatives are available. To enhance usability, the model is provided in various ready-to-use formats and is accessible via the SIMANFOR simulation platform. Despite its strengths, further efforts are required to improve height predictability and deepen the understanding of height variability among stand characteristics. These enhancements would promote the model's transferability and facilitate its adoption by forest managers, thereby supporting decision-making processes.

Abbreviations

- AIC: Akaike Information Criterion
- dbh: tree diameter at breast height (1.30 m)
- dg: quadratic mean diameter
- g: tree basal area
- G: stand basal area
- h: tree height
- h–d: height–diameter ratio
- max: maximum
- MB: mean bias
- min: minimum
- NFI: National Forest Inventory
- RMSE: Root Mean Squared Error
- SFNI: Spanish Forest National Inventory

CRediT authorship contribution statement

Aitor Vázquez-Veloso: Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Data curation. **Sheng-I Yang:** Writing – review & editing, Supervision, Methodology, Formal analysis, Conceptualization. **Bronson P. Bullock:** Supervision, Funding acquisition. **Felipe Bravo:** Supervision, Methodology, Funding acquisition, Conceptualization.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this paper, the authors used generative AI tools to improve the comprehensibility of the manuscript. After using this tool, the authors reviewed and edited the content as necessary and take full responsibility for the content of the publication.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary material related to this article can be found online at https://doi.org/10.1016/j.foreco.2025.122981.

Data availability

Data, code and additional resources are available here:

A repository with the original data, code and results of: *One model t o rule them all: a nationwide height--diameter model for 91 Spanish f orest species* (Original data) (GitHub + Zenodo)

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