Wood density variation in European forest species: drivers and implications for multiscale biomass and carbon assessment in France

Henri Cuny[1], Jean-Daniel Bontemps[2], Nikola Besic[2], Antoine Colin[1], Lionel Hertzog[2], Amaël Le Squin[1],
William Marchand[3], Cédric Vega[2], Jean-Michel Leban[4]

[1]IGN, Service de l'Information Forestière, Champigneulles, F-54250, France
[2]ENSG, UGE, IGN, Laboratoire d'Inventaire Forestier, Nancy, F-54000, France
[3]IGN, Service de l'Information Forestière, Nogent-sur-Vernisson, F-45290, France
[4]INRAE, BEF, Champenoux, F-54280, France

Correspondence to: Henri Cuny (henri.cuny@ign.fr)

Abstract. Wood density is a key parameter for estimating forest biomass and carbon stocks. However, the magnitude and the drivers of wood density variation in temperate forests, and the implications of this variation for biomass and carbon assessments, are not well understood. This study provides a comprehensive analysis of wood density variation in trees of western temperate Europe and evaluates its impacts on forest aboveground biomass (AGB) estimates at multiple spatial scales. From an initial dataset comprising wood density measurements from 110,763 individual trees, representing 156 species across mainland France, we analysed a subset of 44 species accounting for 97% of the growing stock and providing sufficient observations for modelling. We developed linear models of wood density based on tree, stand, site, and climatic variables, and successively examined the contributions of taxonomic identity, environmental factors and their interactions. We also constructed a model using variables potentially accessible through spatial layers (i.e., GIS-based data) at broad scales and fine resolutions, to assess their predictive capacity. Models were applied to French National Forest Inventory (NFI) data to estimate aboveground biomass (AGB) across four spatial scales: the national level, biogeographical regions and subregions (both delineated through biophysical partitioning of the territory) and individual NFI plots. Our analysis revealed that variation in wood density stemmed primarily from interspecific differences (78.5% of the total variance), with the remaining 21.5% attributable to intraspecific variability. Our best performing model—combining variables on species identity, tree dimensions, stand structure, site conditions and climate—explained 82% of total wood density variation, though it captured only a modest portion of intraspecific variability, found mainly driven by tree dimensions and mean annual temperature. In contrast, the model relying solely on environmental factors and the one based on GIS-layer variables accounted for 14% and 34% of the variation, respectively. While accounting for wood density variation had minimal impact on national-scale AGB estimates, it caused deviations of up to 30% at finer scales, such as biogeographical subregions and individual NFI plots. These findings highlight the importance of incorporating wood density variation into forest biomass and carbon assessment, especially at

regional to local scales. Given its dominant role, we recommend integrating species identity as much as possible to enhance the accuracy of forest biomass and carbon stock assessment across spatial scales.

1 Introduction

35   Wood is a major component of terrestrial biomass (Groombridge and Jenkins, 2002), underpinning a wide range of ecological and economic functions (Chave et al., 2009), and mediating some of the largest carbon fluxes between land and atmosphere (Friedlingstein et al., 2023; Pan et al., 2024). A defining feature of wood is its intrinsic variability: properties such as colour, odour, texture, and density can vary markedly—not only between species, but also among individuals of the same species, and even within a single tree (Zobel and van Buijtenen, 1989). Among these traits, basic wood density—defined as the ratio of

40   oven-dry mass to green volume and hereafter referred to simply as wood density—is particularly important and highly variable (Zobel and van Buijtenen, 1989). In Europe, for example, wood density ranges from less than $300 \, \text{kg m}^{-3}$ in species like *Salix alba*, to around $600 \, \text{kg m}^{-3}$ in *Fagus sylvatica*, and exceeds $800 \, \text{kg m}^{-3}$ in *Quercus ilex* (Cuny et al., 2025; Zanne et al., 2009).

The evolutionary history of trees and their species identity are prominent determinants of global variation in wood density

45   (Chave et al., 2006; Kerfriden et al., 2021; Li et al., 2024). Nonetheless, climatic variables such as regional variation in mean annual temperature and soil moisture do shape the global distribution of wood density, primarily through their effects on species composition and assemblage patterns (Mo et al., 2024; Yang et al., 2024). Wood density is also closely linked to species' demographic strategies: fast-growing species typically exhibit lower wood density than slow-growing ones (Chave et al., 2009; Fajardo et al., 2024; Nascimento et al., 2005; Sullivan et al., 2025).

50

At the intraspecific level, wood density varies with tree dimensions (Lachenbruch et al., 2011) and environmental conditions (Chave et al., 2009), particularly climate (Bouriaud et al., 2015; Dalla-Salda et al., 2009). For instance, maximum wood density has been shown to correlate with inter-annual variation in warm seasonal temperatures in several species, making it a valuable proxy for reconstructing past climates (Briffa et al., 1998; Hughes et al., 1984). Wood density is also linked to tree growth rate

55   within species (Guilley et al., 2004; Saranpää, 2003; but see Fajardo et al., 2024; Fajardo, 2016), a relationship that has been used to predict wood properties in silvicultural planning (Houllier et al., 1995).

Because it reflects the amount of dry matter per unit volume, wood density is the key parameter for converting tree volume into biomass, and subsequently into carbon stocks, based on assumptions about carbon content (Doraisami et al., 2024). It thus

60   plays a central role in standard calculation methodologies (Baker et al., 2004; Chave et al., 2004). While tree volume can be relatively easily estimated from external measurements such as stem diameter and height (Vallet et al., 2006), determining wood density requires additional sampling and laboratory analysis. As a result, despite its known variability, wood density is often simplified or overlooked in forest biomass and carbon assessment. Interspecific variation is sometimes partially

accounted for, but intraspecific variation is generally ignored. For instance, in the Land Use, Land-Use Change, and Forestry
65   (LULUCF) sector of IPCC national greenhouse gas inventories, Tier 1 guidelines provide average wood density values at the
species or genus level (see Table 4.13 in Eggleston et al., 2006).

The Global Wood Density (GWD; Chave et al., 2009; Zanne et al., 2009) and Plant Trait (TRY; Kattge et al., 2020) databases
currently represent the most comprehensive global datasets on wood density, covering approximately 8,000 and 11,000
70   species, respectively. Their broad taxonomic and geographic scope is a major strength. However, these datasets compile values
from heterogeneous sources, often based on limited and uneven sampling, and using sometimes poorly documented
methodologies. This limits their ability to capture intraspecific variation and leads to data gaps, particularly for rare or
regionally specific species (Flores and Coomes, 2011; Jenkins et al., 2003).

In France, national estimates of forest biomass and carbon stocks have so far relied on wood density values derived from an
75   unpublished dataset (CARBOFOR project; Loustau, 2002). Some of these values originate from a 170-year-old source
(Mathieu, 1855), updated to provide a single average value per species across approximately 50 species. However, these
estimates are based on small and unbalanced samples—typically fewer than 10 mature trees per species—and fail to capture
the diversity of conditions encountered in French forests, including variability in tree species, tree size, and environmental
80   factors. This raises concerns about the accuracy and representativeness of the resulting biomass and carbon stock estimates.

Besides national inventories, remote sensing technologies are increasingly employed to map the spatial distribution of forest
biomass and carbon (Liu et al., 2023; Santoro and Cartus, 2024; Schwartz et al., 2023). These approaches often rely on canopy
height estimates derived from lidar or radar data (Pellissier-Tanon et al., 2024), which are converted into volume and biomass
85   using allometric equations (Liu et al., 2023; Ma et al., 2024; Schwartz et al., 2023; Yang et al., 2022) or machine learning
models (Su et al., 2025). However, this conversion is typically based on fixed assumptions that overlook wood density
variability, introducing substantial uncertainties (Chave et al., 2019; Labrière et al., 2023) and, in some cases, systematic biases
in biomass estimates (Phillips et al., 2019; Sæbø et al., 2022). As such, improving our understanding of wood density
variation—both within and among species—is increasingly recognised as a critical step toward enhancing the accuracy of
90   forest biomass and carbon mapping (Sæbø et al., 2022).

Although several recent studies have investigated wood density variation, most have concentrated on interspecific differences
at the global scale (Mo et al., 2024; Yang et al., 2024) or within tropical forest ecosystems (Phillips et al., 2019; Sullivan et
al., 2025). In contrast, the present study addresses wood density variation in temperate forests by explicitly disentangling
95   interspecific and intraspecific components, and assessing for their impacts on forest biomass estimates at different spatial
scales.

To this end, we used the *XyloDensMap* dataset, which comprises wood density measurements for 110,763 individual trees sampled across a network of forest plots evenly distributed throughout mainland France (Cuny et al., 2024, 2025). Based on

100 this extensive and spatially representative dataset, our study pursued four main objectives: (1) quantify variation in wood density at the interspecific and intraspecific levels across temperate forest species; (2) identify and measure the intensity of the biotic and abiotic drivers of this variation; (3) map how this variation translates into the spatial distribution of wood density; (4) evaluate the impact of accounting for this spatial distribution on biomass and carbon estimates at multiple spatial scales.

105 To address these objectives, we developed linear models incorporating tree, stand, site, and climate variables. Models were used to quantify wood density variation at both interspecific and intraspecific levels and to identify its main drivers. They were subsequently applied to predict wood density for the 1,221,584 trees measured by the French National Forest Inventory (NFI) between 2005 and 2022. This enabled us to map wood density distribution across France and estimate aboveground forest biomass at four distinct spatial scales: national totals, totals for biogeographical regions and subregions—both delineated

110 through biophysical partitioning of the territory—and individual NFI forest plots.

2 Data and methods

2.1 Dataset

2.1.1 The *XyloDensMap* dataset

The *XyloDensMap* open dataset comprises individual wood density measurements from 110,763 wood increment cores

115 collected at breast height in mainland France (Cuny et al., 2024, 2025). Data were obtained by combining the spatially systematic sampling design of the French National Forest inventory (NFI) and a high-throughput method of wood density measurement by X-ray Computed Tomography (Freyburger et al., 2009; Jacquin et al., 2019). Owing to the systematic nature of the NFI's annual sampling framework (Bontemps and Bouriaud, 2024; Bouriaud et al., 2023), the *XyloDensMap* dataset is representative of the French forest, especially in terms of species diversity and tree size distribution (Cuny et al., 2025). Full

120 details on sampling design, sample processing and wood density measurement are provided in the corresponding data descriptor (Cuny et al., 2025).

The *XyloDensMap* dataset provides four different wood density values, depending on whether anhydrous or green volume is used as a reference, and whether or not a weighting method is applied to calculate an average wood density representative of

125 the entire stem cross-section (Williamson and Wiemann, 2010). The weighted mean basic wood density (hereafter called wood density) was used here. It corresponds to the ratio of dry mass to green volume that can be used for effective conversion of tree green volume into dry biomass under the assumption of the homogeneity of wood density in the whole tree (but see Billard et al., 2021).

2.1.2 Variables used to model wood density

130   The French NFI acquires tens of variables related to tree, stand, soil and flora characteristics. Based on correlation analysis (with consideration of the variance inflation factors, see below) and current knowledge of the drivers of wood density variability (see, e.g., Bergès et al., 2008; Bouriaud et al., 2004, 2015; Franceschini et al., 2013; Guilley et al., 2004; Mo et al., 2024; Yang et al., 2024), an initial selection was made on these variables to retain a subset of 17 variables available for all trees inventoried by the French NFI and of potential interest for modelling wood density (Table 1). Given that

135   tree dimensions such as diameter at breast height (DBH) and total height are highly correlated with each other, we decided to rather use DBH and an indicator of tree slenderness, as estimated from the ratio between the total tree height (in m) and the square root of DBH (in cm) (Vallet et al., 2006).

In addition, two climatic normals (mean annual temperature and total annual precipitation averaged over the 1991-2020 period)

140   were extracted at a kilometric resolution (Météo France, AURELHY model; see Canellas et al., 2014) for each sample plot location. Thus, a total of 19 variables encompassing tree, stand, site, and climate characteristics were identified and considered for modelling wood density (Table 1; see Supplementary Table S1 for details on each variable calculations).

Table 1: Overview of the 19 candidate variables considered for wood density modelling. The column "Accessible via GIS layers"
145 **specifies whether each variable is restricted to local availability (e.g., National Forest Inventory plots) or could be accessed more**
broadly and at finer spatial resolution via geographic information systems (GIS) layers.

Type of variable	Variable	Unit	Type	Signification	Source	Accessible via GIS layers
Species identity	Botanical class	-	Categorical	Tree botanical class (broadleaf or conifer)	NFI	No
	Genus	-	Categorical	Tree genus	NFI	No
	Species	-	Categorical	Tree species	NFI	No
Tree dimensions	RW5	mm	Continuous	Average width of the last five tree rings	NFI	No
	DBH	cm	Continuous	Tree diameter at breast height	NFI	No
	SLD	-	Continuous	Tree slenderness, as estimated by the ratio between the tree height (in m) and the square root of the diameter at breast height (in cm)	NFI	No
	BAL	m²	Continuous	Competition index calculated as the sum of the basal areas of all trees with a diameter at breast height (DBH) greater than that of the subject tree	NFI	No
Stand attributes	N	trees ha^{-1}	Continuous	Number of trees per hectare in the stand	NFI	No
	G	m² ha^{-1}	Continuous	Basal area per hectare of the stand	NFI	No
	DQ	cm	Continuous	Quadratic mean diameter of the stand	NFI	No
	HDOM	m	Continuous	Dominant height of the stand (mean height of the 100 tallest trees per hectare)	NFI	Yes
	VSTR	-	Categorical	Vertical structure of the stand	NFI	Yes
	COMP	-	Categorical	Forest composition type as estimated from the French "BD Forêt" map	NFI	Yes
Site characteristics	TRO	-	Discrete	Trophic level index	NFI	No
	RAD	-	Discrete	Solar radiation index	NFI	No
	SWC	mm	Continuous	Soil water capacity	NFI	No
	BSR	-	Categorical	Biogeographical subregion	NFI	Yes
Climate conditions	TM	°C	Continuous	Mean annual temperature	Météo France	Yes
	P	mm	Continuous	Total annual precipitation	Météo France	Yes

2.1.3 Data processing

The *XyloDensMap* dataset contains wood density records obtained from wood increment cores that can represent different
150 proportions of the tree radius. Given the radial variability of wood density within stems (Lachenbruch et al., 2011), we retained
only those increment cores that represented more than 50% of the tree radius (amounting to 78,377 out of 110,763 cores) to
ensure a more representative estimate of stem wood density.

Due to the systematic sampling of the French NFI, the number of wood density measurements in the *XyloDensMap* dataset is
155 proportional to the abundance of tree species across space, which varies strongly (Bontemps et al., 2019), and has immediate
consequence on the number of wood density measurements available for each species (Cuny et al., 2025). Because of this
unbalanced distribution, models were built for a subset of species showing at least 150 wood density measurements for the
sake of model training and testing. This resulted in a dataset with 75,256 individual wood density values for 44 tree species.
Availability of the 19 candidate predictors and removal of a few outlier values (defined as exceeding four standard deviations
160 above and below the mean) led to discard an additional 1,107 wood density records, to reach 74,149 wood density values in
the final subset of data considered for modelling (Supplementary Table S2).

Selected species covered different wood structures types, with nine conifer species (tree rings mainly composed of tracheids
with decreasing cell-diameter and increasing wall-thickness from early- to latewood) and 35 broadleaf species, including nine
165 ring-porous species (tree rings containing many wide vessels in earlywood marking a sharp transition with dense latewood),
12 diffuse-porous species (vessels of similar size evenly distributed across a tree ring), and 14 semi ring-porous species
(intermediate structure between ring-porous and diffuse-porous species). Selected tree species ensure a 97% coverage of the
forest growing stock in mainland France (as estimated with the French NFI data from the 2016-2019 collection years and the
NFI estimation process, which can be run online at https://ocre-gp.ign.fr/ocre).

170 **2.1.4 Preliminary data exploration**

All analyses presented in this study were performed using the R statistical software version 4.3.2 (R Core Team, 2023).

The mean wood density in the final selected dataset was 575 ± 112 kg m^{-3} (mean $\pm$ standard deviation), with individual values
ranging from approximately 200 kg m^{-3} to over 1,000 kg m^{-3}. On average, broadleaf species exhibited higher wood density
than conifers (612 ± 92 vs 438 ± 63 kg m^{-3}). Boxplots by species highlighted large interspecific variation, with a gradient
175 among broadleaf species from low-density genera such as *Populus*, *Tilia*, and *Alnus*, to high-density genera like *Quercus*
(Supplementary Figure S1). Wood density ranged from 381 ± 47 kg m^{-3} in *Populus* spp. to 854 ± 67 kg m^{-3} in *Quercus ilex*.
Among conifers, species from the genera *Abies* and *Picea* exhibited lower wood density compared to those from *Pinus*, and
wood density ranged from 387 ± 44 kg m^{-3} in *Picea abies* to 534 ± 42 kg m^{-3} in *Pinus halepensis*.

180

These boxplots also revealed substantial intraspecific variation. For example, wood density in *Quercus petraea*—the broadleaf
species with the largest growing stock in mainland France—ranged from 436 kg m^{-3} to 890 kg m^{-3}. Similarly, *Abies alba*, the
conifer species with the largest growing stock, showed wood density values ranging from 263 to 605 kg m^{-3}. Density plots
indicated that within each species, wood density followed a unimodal, bell-shaped distribution (Supplementary Figure S2).

185

Preliminary exploration of the covariate data shows moderate collinearity among a limited number of variables (Supplementary Figure S3). It also revealed potentially non-linear relationships between wood density and the variables related to tree dimensions (average width of the last five rings, tree diameter, tree slenderness, and basal area of larger trees), associated to a right-skewed distribution of these variables. A logarithm transformation of the predictors linearised the relationships and ensured more centred distributions (Supplementary Figure S4).

Correlation analyses revealed species-specific relationships between wood density and candidate variables, particularly those related to tree dimensions (notably average width of the last five rings, tree diameter and slenderness; Supplementary Table S3). For example, the relationship between wood density and the average width of the last five tree rings was systematically positive in ring-porous broadleaf species and always negative for conifers, while for semi-ring porous and diffuse porous broadleaf species the direction of the relationship was negative or positive depending on the species.

2.2 Modelling approach

To detect the drivers of wood density variation and the magnitude of their effects, we fitted four linear models using the *lm* function in R, each incorporating different combinations of explanatory variables (Figure 1). These models span a gradient of input type and resolution, from those leveraging fine attributes uniquely available through NFI field plot data, such as detailed tree- and stand-level characteristics, to models relying exclusively on coarser ecological and forest descriptors potentially accessible via GIS-layer data for remote sensing applications. This modelling framework was designed to disentangle the contributions of different predictive drivers and to assess how data type and granularity influence the accuracy of wood density estimates.

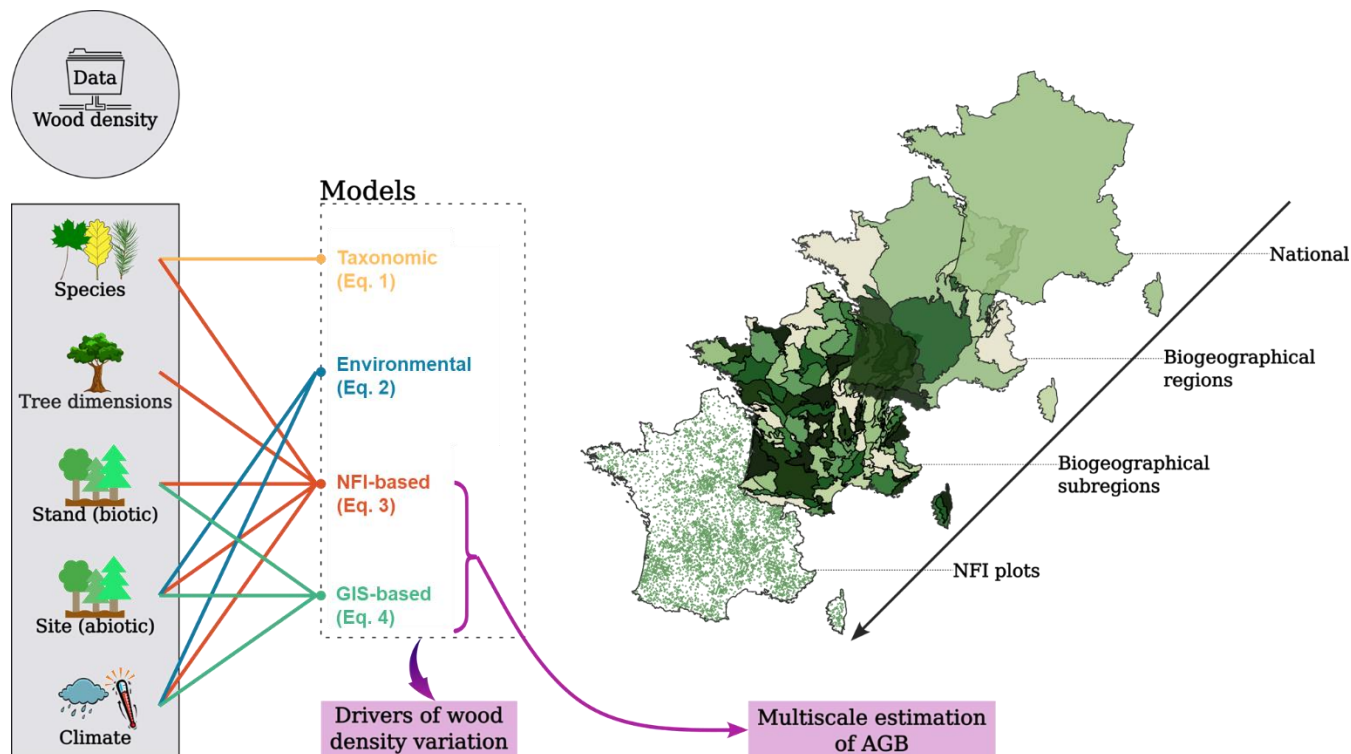



Figure 1: Overview of the modelling framework. Data on wood density (dependent variable) and a suite of tree-, stand-, site-, and climate-level variables (shown in grey rectangle) were used to develop four statistical models aimed at identifying the main drivers of wood density variation. In parallel, two of these models (the "NFI-based model" and the "GIS-based model"), alongside a single
210 **mean coefficient, were applied to the French National Forest Inventory (NFI) data to predict wood density values and calculate forest aboveground biomass (AGB) stocks across four spatial scales.**

2.2.1 Taxonomic model

To characterise interspecific variation in wood density and evaluate taxonomic influence, we developed a first linear model
215 (hereafter referred to as the "taxonomic model") incorporating the three following hierarchical taxonomic levels: botanical class, genus, and species. The model was expressed as follows:

$$WD_i = \alpha + \beta 1_{bc[i]} + \beta 2_{g[i]} + \beta 3_{sp[i]} + \varepsilon_i, \tag{1}$$

where WDi is the wood density of individual i, α is the model intercept, and β1, β2, and β3 are the coefficients associated with botanical class (bc), genus (g), and species (sp), respectively. The residual error term ε_i is assumed to be normally distributed.
220 To quantify the relative contribution of each taxonomic level to interspecific variability, we conducted a Type I analysis of variance (ANOVA) on this model using the *anova* function in R.

2.2.2 Environmental model

Environmental factors can influence wood density both interspecifically—through species composition—and intraspecifically—via tree development and stand conditions. To assess these effects independently of species identity, tree dimensions and stand characteristics, we constructed a second model (hereafter referred to as the "environmental model") using only site and climate variables. The model was formulated as:

$$WD_i = \alpha + \beta1 \times TRO_i + \beta2 \times RAD_i + \beta3 \times SWC_i + \beta4 \times TM_i + \beta5 \times P_i + \varepsilon_i, \tag{2}$$

with WD_i the wood density of individual i, α the model intercept, and β1, β2, β3, β4, and β5 the model coefficients associated with the covariates site trophic index (TRO), solar radiation (RAD), soil water capacity (SWC), mean annual temperature (TM) and total annual precipitation (P). ε_i is the normally distributed residual error term.

2.2.3 NFI-based model

To identify the most influential drivers of wood density variation, we developed a third model (hereafter referred to as the "NFI-based model") combining species identity and environmental descriptors along with detailed NFI variables related to tree- and stand-characteristics. Stand dominant height was excluded due to its correlation with tree slenderness and was instead incorporated into a separate model (see below). By comprehensively combining detailed variables at the individual tree and stand scale, this model aimed to achieve the highest possible precision in explaining wood density variation.

Log-transformations were applied to variables related to tree dimensions (RW5, DBH, SLD, BAL) to linearise relationships and normalise distributions. For zero RW5 values (representing trees with ring widths thinner than the field measurement resolution), we applied the transformation *log* (RW5 + 0.1), with 0.1 corresponding to field measurement resolution. Likewise, *log* (BAL + 1) was used to accommodate zero BAL values (which represent the largest tree on the plot). To account for species-specific effects, interaction terms between tree species and each continuous predictor were incorporated. The model took the following form:

$$WD_i = \alpha_{sp[i]} + \beta1_{sp[i]} \times \log(RW5_i + 0.1) + \beta2_{sp[i]} \times \log(DBH_i) + \beta3_{sp[i]} \times \log(SLD_i) + \beta4_{sp[i]} \times \log(BAL_i + 1) +$$
$$\beta5_{sp[i]} \times N_i + \beta6_{sp[i]} \times G_i + \beta7_{sp[i]} \times DQ_i + \beta8_{sp[i]} \times TRO_i + \beta9_{sp[i]} \times RAD_i + \beta10_{sp[i]} \times SWC_i + \beta11_{sp[i]} \times TM_i +$$
$$\beta12_{sp[i]} \times P_i + \varepsilon_i, \tag{3}$$

with WD_i the wood density of individual i, α the model intercept for the tree of species sp, and β1, β2, β3, … the species-specific coefficients associated with the covariates (RW5, DBH, SLD, …) that can be found in Table 1. ε_i is the normally distributed residual error term. We assessed multicollinearity using the variance inflation factors (VIFs) computed with the vif function from the R package *car* (Fox and Weisberg, 2019). All VIF values for the selected predictors were below 5, indicating acceptable levels of collinearity.

2.2.4 GIS-based model

255 A fourth model (hereafter referred to as the "GIS-based model") was developed using variables potentially available at the national scale and at high spatial resolution through GIS layers. This model aimed to assess the feasibility of reconstructing wood density variation without relying on detailed tree- or stand-level descriptors such as those provided by NFI data. In addition to mean annual temperature and total annual precipitation, four other variables were included, selected either for their current availability or potential to be represented through GIS layers: stand dominant height (defined as the mean height of the

260 100 tallest trees per hectare), vertical stand structure (four classes determined from NFI data: regular forest, irregular forest, coppice, forest-coppice mix), stand composition, and biogeographical subregion. Stand dominant height and vertical structure were derived from NFI field data but could also be estimated through remote sensing methods (Besic et al., 2025; Martin-Ducup et al., 2025; Schwartz et al., 2023). Stand composition and biogeographical subregions are already available for the entirety of mainland France. Stand composition is provided by the "BD Forêt", an open access map based on aerial photograph

265 analyses that classifies forest cover into 32 forest types (https://www.data.gouv.fr/fr/datasets/bd-foret-r/). Biogeographical subregions—86 classes in total—are defined by the French NFI as "sufficiently large geographical areas within which the combination of values taken by the factors determining forest production or the distribution of forest habitats is original" (Cavaignac, 2009; https://inventaire-forestier.ign.fr/spip.php?rubrique267). The "GIS-based model" was expressed as follows:

$$WD_i = \alpha + \beta 1_{vstr[i]} + \beta 2_{comp[i]} + \beta 3_{bsr[i]} + \beta 4 \times TM_i + \beta 5 \times P_i + \beta 6 \times HDOM_i + \varepsilon_i, \tag{4}$$

270 with WD_i the wood density of individual i, α the model intercept, β1, β2, β3 the model coefficients associated with the categorical covariates stand vertical structure (vstr), stand composition (comp) and biogeographical subregion (bsr), and β4, β5, β6 the model coefficients associated with the continuous covariates mean annual temperature (TM), total annual precipitation (P), and stand dominant height (HDOM). ε_i is the normally distributed residual error term.

2.2.5 Model evaluation

275 For all models, the dataset was partitioned at species level into 80% for model training and 20% for model testing. Partitioning was carried out using the *createDataPartition* function of the R package *caret* (Kuhn and Max, 2008). Performance of models was assessed by computing the mean absolute error (MAE, Willmott and Matsuura, 2005), the mean absolute percentage error (MAPE, Armstrong and Collopy, 1992) and the coefficient of determination or R-squared (R^2, Mayer and Butler, 1993). In order to assess the importance of variables in models, we computed the Lindeman, Merenda and Gold (lmg) index using the

280 *relaimpo* package in R (Groemping, 2006). The index provides the relative contribution of each predictive variable to the R-squared with the consideration of the sequence of variables appearing in the model.

2.3 Model application

2.3.1 Predicting wood density on French NFI data

We computed wood density for the French National Forest Inventory (NFI) dataset—comprising 1,221,584 trees across
285 104,199 plots inventoried between 2005 and 2022 in mainland France—using three distinct approaches that reflect a gradient
in how wood density variability is incorporated into aboveground biomass (AGB) estimates. First, we used the "NFI-based
model" described in Eq. (3), which provides a detailed representation of wood density variation based on tree-, stand-, site-,
and climate-level information. Second, we applied the "GIS-based model" outlined in Eq. (4), which captures wood density
variation using coarser, yet highly resolved, predictors potentially accessible via GIS layers. Lastly, we applied a constant
290 mean wood density uniformly across all trees, thereby ignoring wood density variation. This mean value was derived from the
XyloDensMap dataset, based on wood density measurements from increment cores covering more than 50% of the tree radius.

The "taxonomic model" and "environmental model" were excluded from direct prediction: the "taxonomic model" served to
explore species identity and its influence (integrated into the "NFI-based model"), while the "environmental model" was used
295 to isolate environmental effects (also integrated in the "NFI-based model" and in the "GIS-based model").

Models enabled wood density predictions for 97% of the trees in the NFI dataset. For the remaining 3%—trees belonging to
species for which no model was developed—we used species-specific mean wood density values calculated from the
XyloDensMap dataset (based on increment cores covering more than 50% of the tree radius). For rare species present in the
300 NFI data but not covered in the *XyloDensMap* dataset (0.04% of trees), we used genus-level averages (0.01% of trees), or,
when genus-level data were unavailable, botanical class-level averages (broadleaf or conifer; 0.03% of trees).

2.3.2 Estimating aboveground biomass at multiple scales in French forests

We used the three types of predicted wood density ("NFI-based model" predictions, "GIS-based model" predictions, constant
mean) to calculate the aboveground biomass (AGB) of each tree inventoried by the French NFI using the following Eq. (5):

305 $$AGB_i = 0.001 \times AGV_i \times WD_i, \tag{5}$$

where AGB is the tree aboveground biomass of individual i (in tons), AGV is the tree aboveground volume (stem and branches;
in m^3) calculated by French NFI using allometric equations (Vallet et al., 2006), and wood density is the corresponding wood
density predicted according to one of the three approaches (in kg m^{-3}).

310 The three AGB values calculated for each tree using the different wood density estimates were then integrated into the standard
NFI processing workflow to estimate forest AGB stocks at four spatial scales: (1) at the national level; (2) across the 11
biogeographical regions and (3) 86 biogeographical subregions delineated by the French NFI based on biophysical partitioning

of the territory (Cavaignac, 2009); and (4) for each of the 104,199 forest plots (700 m² each) inventoried by the French NFI from 2005 to 2022 (Figure 1).

2.3.3 Mapping wood density in France

The wood density predicted using the "NFI-based model" for each tree recorded in the NFI dataset was further used to calculate a community-wide mean wood density (CWD; Swenson and Enquist, 2007) for each NFI forest plot, in order to assess the implications of the spatial distribution of wood density on forest AGB assessments. To do this, estimated individual wood density values were averaged at the plot level, taking into account the weight of each tree in the statistical sampling (as provided by the French NFI) as well as the total aerial volume of each tree:

$$CWD = \frac{\sum_{i=1}^{n}(WD_i \times AGV_i \times w_i)}{\sum_{i=1}^{n}(AGV_i \times w_i)}, \tag{6}$$

where CWD is the community-wide mean wood density (in kg m^{-3}) for a plot of n individuals scaled to per hectare, WD$_i$ is the predicted wood density (in kg m^{-3}) using the "NFI-based model", AGV$_i$ is the aboveground volume (in m^3) and w$_i$ is the statistical weight in NFI sampling design (in number of stems ha^{-1}) of the ith tree.

3 Results

3.1 Drivers of wood density variation

3.1.1 Taxonomic influence on wood density variation

The "taxonomic model" presented in Eq. 1 revealed that the botanical class alone explained 40.1% of the variance in wood density. The finer levels (genus and species) contributed an additional 38.4% of variance, with genus alone representing 30.8% (Supplementary Table S4; yet, 32% of studied species were alone in their genus). Altogether, species-level taxonomic information therefore explained 78.5% of the total variation in wood density, highlighting the dominant role of interspecific differences. The remaining 21.5% reflects intraspecific variability.

3.1.2 Environmental influence on wood density variation

The "environmental model" presented in Eq. 2 was intended to isolate the influence of environmental factors on wood density, deliberately excluding those related to species identity, tree dimensions, and stand structure. This model accounted for 14% of the total variation in wood density, underscoring the limited explanatory power of environmental descriptors when considered in isolation. Among these, mean annual temperature exhibited a strong positive effect, increasing wood density by approximately 19.8 ± 0.3 kg m^{-3} per degree Celsius. Variable importance analysis identified mean annual temperature as the most influential factor in this model, with a relative importance of 59%. It was followed by the trophic index (22%) and total

340 annual precipitation (16%), while soil water capacity and solar radiation contributed only marginally (2% and 1%, respectively).

3.1.3 Identifying the main drivers of wood density variation

Variation in wood density was further analysed using the "NFI-based model" presented in Eq. (3), integrating variables related to tree, stand- site, and climate. This model explained 82% of the total variance in wood density. Within the 21.5% representing

345 intraspecific variability, 18% remained unexplained, while 3.5% was attributable to interactions between species and covariates, thus accounting for a very modest share of intraspecific variation in wood density.

Results from the variable importance analysis showed that tree dimension variables—specifically the mean width of the last five annual rings, the diameter at breast height, and tree slenderness—were the most influential on intraspecific variation

350 (Figure 2). Mean annual temperature also contributed, though to a lesser extent, while the remaining variables had only marginal explanatory power.

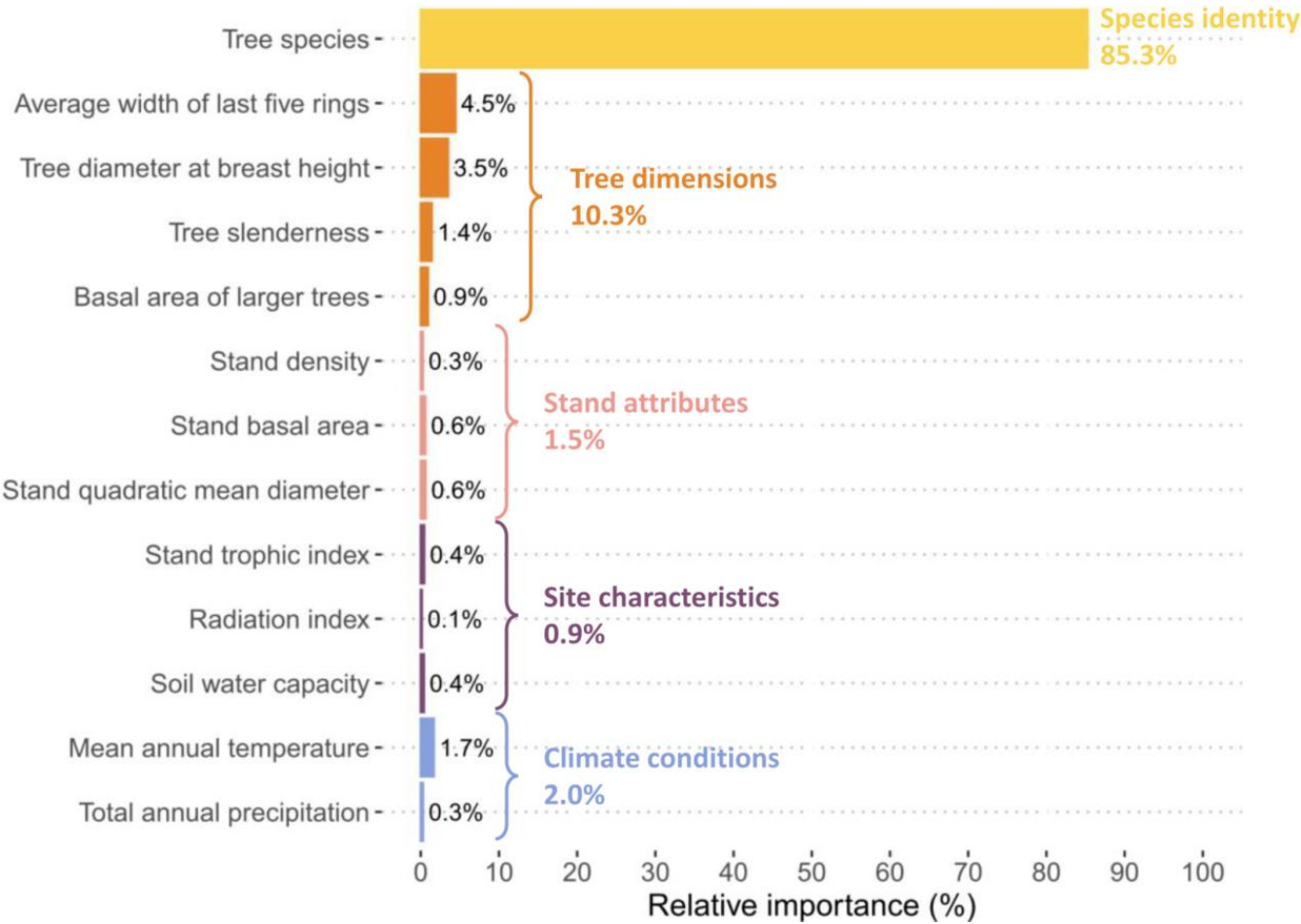



Figure 2: Relative importance (in %) of predictive variables in the "NFI-based model" of wood density variation. Variable
355 **importance was estimated using the lmg method. For each continuous variable, a species-specific interaction term was included in**
the model. For average width of the last five rings, tree diameter at breast height, tree slenderness and basal area of larger trees, a
log-transformation was applied.

3.1.4 Species-specific patterns of wood density variation

360 Looking at intraspecific variation in wood density, the significance of model coefficients in the "NFI-based model" supported

the findings from the variable importance analysis. Across species, tree dimension variables were the most significant

predictors—particularly the average width of the last five rings and tree slenderness, both significant for 32 out of 44 species,

followed by the diameter at breast height, significant for 28 species (see Supplementary Table S5). Mean annual temperature

also showed a strong association with wood density, emerging as a significant predictor in more than half of the species

365 examined (24 out of 44).

All coefficients of the "NFI-based model" are provided in Supplementary Table S6. They revealed clear trends across tree botanical classes or wood structure types. For example, the effect (considering significant effects only) of the average width of the last five rings on wood density was always positive in ring-porous species, but systematically negative in diffuse porous

370 and conifer species (Figure 3). Among semi ring-porous species, the effect was negative solely for *Populus tremula*.

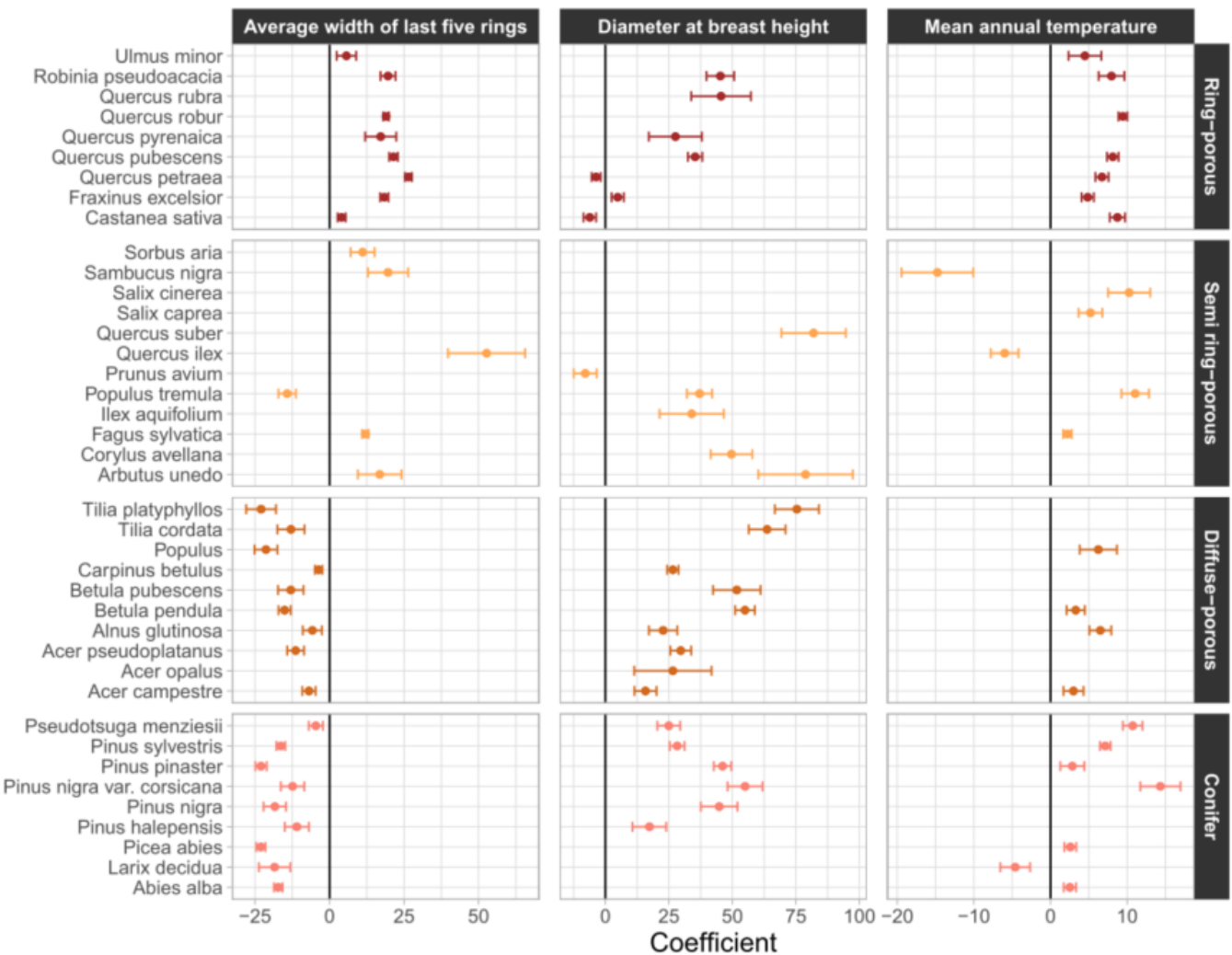



Figure 3: Coefficients affected to the average width of the last five tree rings, the diameter at breast height and the mean annual temperature in the "NFI-based model" of wood density variation. Error bars represent the standard error around coefficients.
375 **Unsignificant coefficients are not shown. For the average width of the last five tree rings and the diameter at breast height, coefficients are for the log-transformed variable.**

Regarding the tree diameter at breast height, the effect on wood density was positive across all species, except for *Castanea sativa*, *Quercus petraea*, and *Prunus avium* (Figure 3). The effect of the tree slenderness was also positive in conifers, and

380   mostly negative in broadleaf species, with the exception of *Arbutus unedo*, *Carpinus betulus* and *Tilia cordata* (Supplementary Table S6).

The effect of mean annual temperature on wood density was found mainly positive across species, except for *Quercus ilex*, *Sambucus nigra* and *Larix decidua* (Figure 3). By contrast, the effect of soil water capacity was negative, with the exception

385   of *Quercus rubra* and *Pseudotsuga menziesii* (Supplementary Table S6). These results suggest that, within species, trees growing in warmer and drier regions tend to produce denser wood compared to those in cooler and wetter environments.

3.1.5 GIS-accessible drivers of wood density variation

The "GIS-based model" presented in Eq. (4) and using only variables potentially available via GIS layers accounted for 34% of wood density variation. According to the lmg method, forest composition type emerged as the most influential predictor,

390   with a relative importance of 50%, in line with results from the "taxonomic model". It was followed by the biogeographical subregion (27%) and mean annual temperature (11%), while stand structure, total annual precipitation and stand dominant height contributed less (5%, 4% and 3%, respectively).

3.2 Model performance in predicting wood density variation

Among the different models evaluated, the "NFI-based model" logically achieved the highest performance (Table 2). It showed

395   strong agreement between train and test datasets (Figure 4), with an R² of 0.82 and a mean absolute error (MAE) of 37 kg m⁻³ (approximately 6%). Reflecting the dominant role of tree species identity on wood density, the "taxonomic model" performed nearly as well, yielding an R² of 0.79 and a MAE of 41 kg m⁻³ (~7%).

Table 2: Performances of the four models tested for modelling wood density variation.

Indicator	Data	Taxonomic model	Environmental model	NFI-based model	GIS-based model
R²	**Train**	0.79	0.14	0.82	0.34
	Test	0.79	0.14	0.82	0.32
MAE (kg.m-3)	**Train**	41	84	37	72
	Test	41	85	37	73
MAPE (%)	**Train**	7.0	14.7	6.4	12.6
	Test	7.0	14.7	6.5	12.7

400

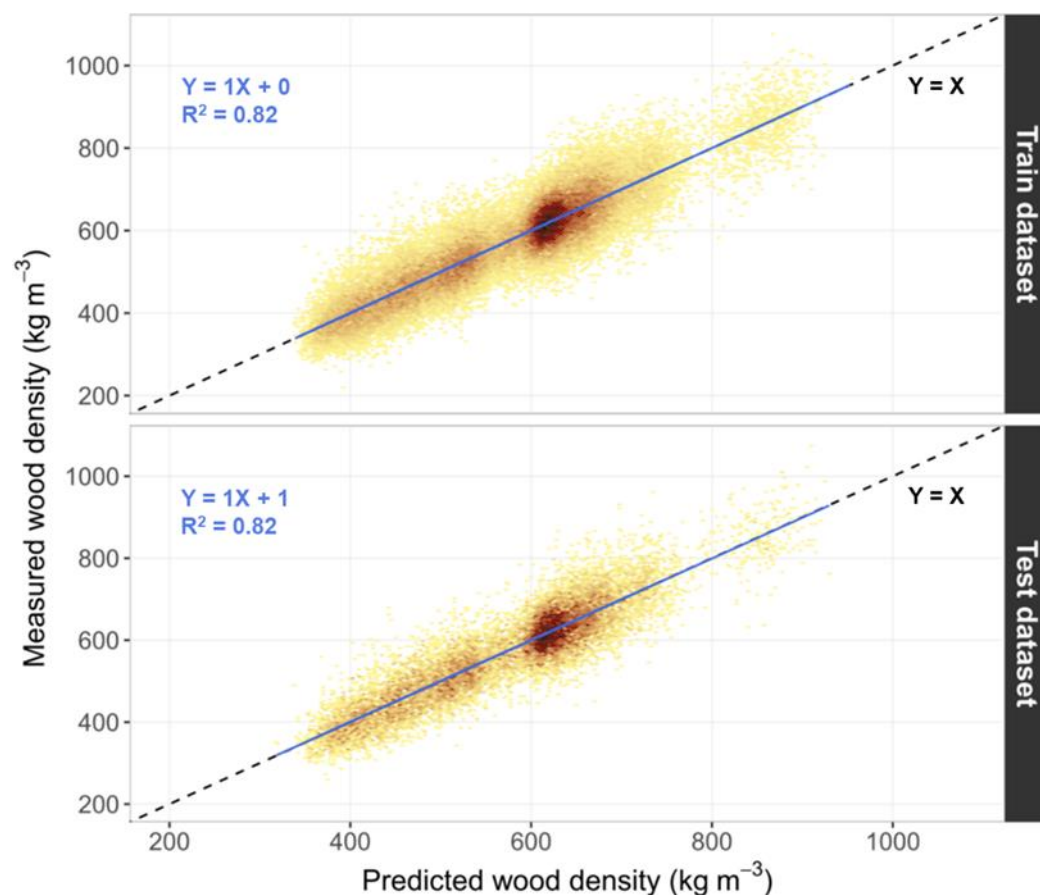



Figure 4: Measured vs. predicted values of wood density on train and test data using the "NFI-based model". Colour depends on the density of points (the darker the colour, the denser the observations). Full blue line: OLS regression line between predicted and measured values, dashed black line: reference Y = X.

405

In contrast, the models lacking detailed tree-level information demonstrated lower performance: the "environmental model" exhibited limited predictive power, with a R² of 0.14 and a MAE exceeding 80 kg m⁻³ (~15%); the "GIS-based model" showed intermediate performance, with an R² just above 0.30 and a MAE slightly over 70 kg m⁻³ (~13%).

3.3 Simulation of wood density on French NFI data

410 Wood density values predicted on NFI data using the "NFI-based model" were consistent with both interspecific and intraspecific variations observed in the *XyloDensMap* dataset (Figure 5; see Supplementary Figure S5 for more detailed results). On the one hand, interspecific variation was accurately reproduced in the simulated values. Among broadleaf species, the simulated values mimicked the trend from dense woods typical of the genus *Quercus* to lower densities found in genera such as *Populus* or *Salix*. For conifers, the simulations reflected the trend from denser woods in *Pinus* species to lighter woods

415 in *Abies* and *Picea*. On the other hand, intraspecific variation was only partially reconstituted, which aligns with the relatively

limited proportion of intraspecific wood density variation captured. In contrast, predictions from the "GIS-based model", while able to reflect general density trends, failed to reproduce interspecific variation (Figure 5), due to the absence of species-level information, which was not captured by the variables included in the model. The latter was found systematically biased across species (magnitude of 62 kg m^{-3} on average), with the bias negatively correlated with wood density, indicating a clear

420   regression toward the mean. This led to bidirectional bias among broadleaved species, while conifers showed exclusively positive bias, suggesting a risk of systematic underestimation of wood density and biomass stocks in coniferous forests.

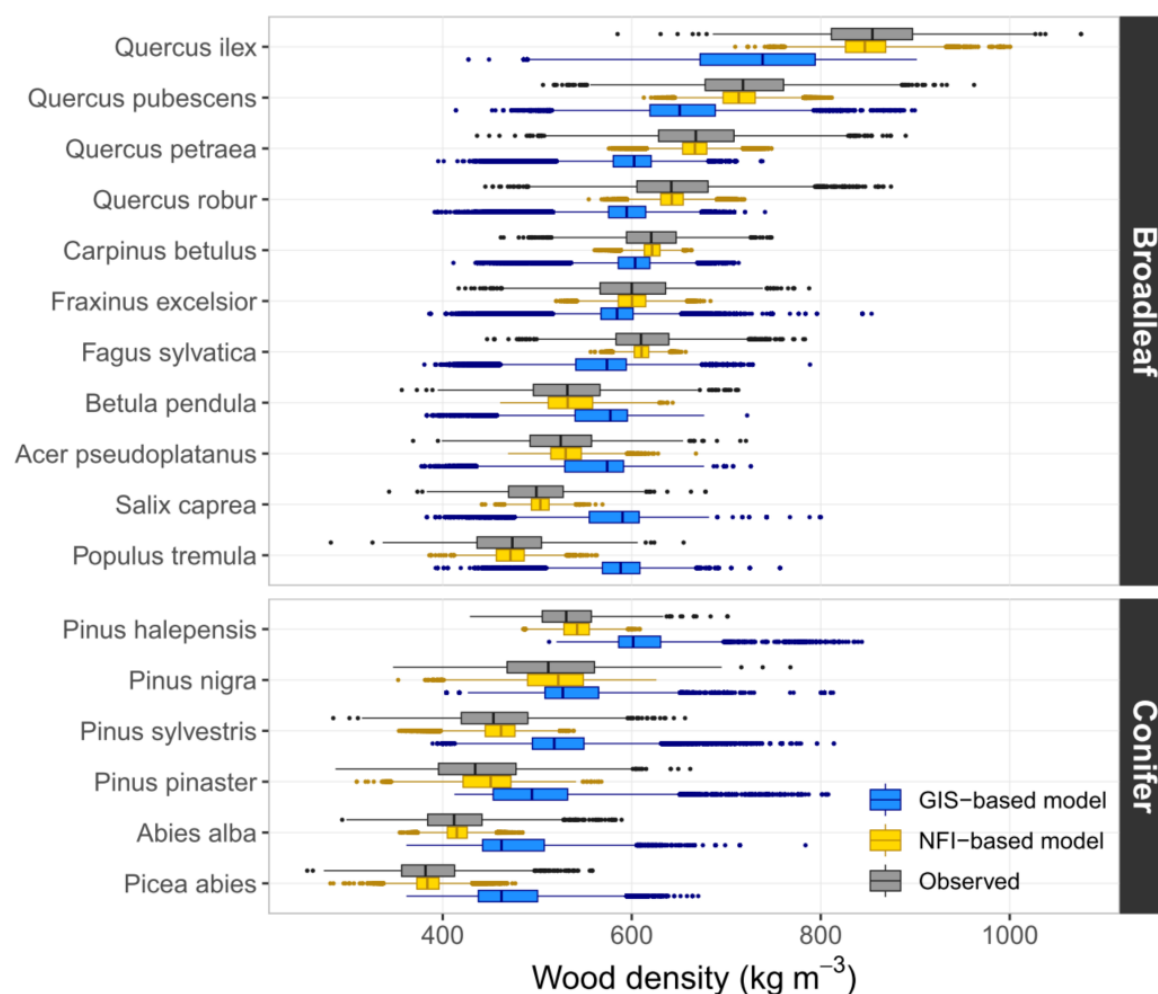
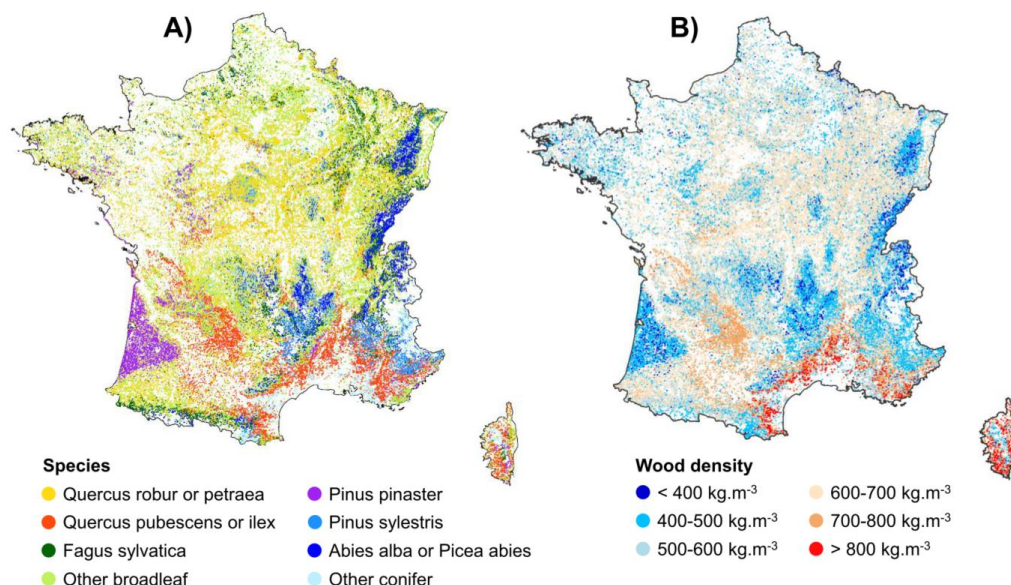



Figure 5: Wood density values predicted on the French NFI dataset and values observed in the *XyloDensMap* data selected for
425   **modelling. Observed values correspond to measurements on wood increment cores, while predicted values were obtained from the "NFI-based model" (orange) and the "GIS-based model" (blue) developed on these measurements. Results are shown for a subset of 17 species.**

3.7 Spatial variation of wood density in mainland France

430   Mapping the community-wide mean wood density (CWD) derived from the individual estimates of the "NFI-based model" applied to forest plots inventoried by the French NFI revealed distinct spatial patterns across mainland France driven largely by forest species composition (Figure 6). Mountainous regions in eastern France or the Aquitaine massif in the southwest, dominated by conifer species (*Abies alba* and *Picea abies* in eastern France, *Pinus pinaster* in south-western France), exhibited notably low CWD values. In contrast, lowland areas dominated by broadleaf species displayed higher CWD. The

435   Mediterranean zone, where broadleaf species characterised by high wood density (notably *Quercus ilex* and *Quercus pubescens*) are prevalent, stood out as a region with particularly elevated CWD. These patterns further underscore the critical role of species-level taxonomic information in explaining wood density variation, in line with previous findings.

440   **Figure 6: Map of species distribution and community-wide mean wood density in mainland France. A) Species distribution map (species with the highest percent canopy cover in the corresponding forest NFI plot) and B) community-wide mean wood density map, based on the wood density predicted by the "NFI-based model" on each forest plot inventoried by the French NFI between 2005 and 2022.**

3.8 Aboveground biomass estimates at multiple scales across French forests

445   The application of different methods to infer wood density on French NFI data led to very similar national estimate of aboveground biomass (AGB) stocks in French forests. The total forest AGB reached approximately 2.4 gigatons of dry biomass, using either the individual wood density values predicted from the models ("NFI-based model" and "GIS-based model"), or the single average coefficient.

450

However, larger differences emerged at finer spatial scales. At the level of the 11 biogeographical regions, the mean absolute difference in AGB between estimates from the "NFI-based model" and those using the constant mean was around 8%. This discrepancy increased to 10–15% in mountainous regions (Vosges, Jura, Alps) and the Mediterranean zone (Figure 7A). At the scale of the 86 biogeographical subregions, differences reached up to 30%, therefore twice as much in magnitude. Notably,

455 biomass estimate discrepancies surpassed 10% in more than 25% of the subregions, and exceeded 20% in just under 10% of them (Figure 7B).

At the NFI forest plot level, the average absolute difference in AGB between estimates derived from the "NFI-based model" and those obtained from the average coefficient was 15%. About 60% of plots exhibited differences greater than 10%, 25%

460 showed differences above 20%, and 13% showed differences exceeding 30% (Figure 7C). Therefore, this difference tended to increase toward lower spatial scales, but remained in a comparable order of magnitude. This was found consistent with the low contribution of site and stand attributes that predominate at plot level, while tree species attributes are structured at a larger spatial scale (see Figure 6).

465 The local magnitude and direction of the differences in AGB depended on the spatial distribution of wood density (Figure 6). As an obvious rule, neglecting wood density variation led to an underestimation of AGB in forests composed of species characterised by high wood density and, on the contrary, to an overestimation of AGB in forests made up of species with low wood density. For example, AGB calculated using a single average coefficient was underestimated in the Mediterranean region populated by broadleaf species with high wood density such as *Quercus ilex* (average wood density = 850 kg m^{-3}; Figure 6;

470 Figure 7C). On the other hand, it was overestimated in regions populated by conifer species with low wood density, such as *Abies alba* (average wood density = 415 kg m^{-3}) and *Picea abies* (average wood density = 387 kg m^{-3}) in eastern France and *Pinus pinaster* (average wood density = 438 kg m^{-3}) in southwestern France (Figure 6; Figure 7C).

Using wood density values predicted by the "GIS-based model" notably reduced discrepancies across all spatial scales. In the

475 11 biogeographical regions, the mean absolute difference in AGB between estimates derived from the "GIS-based model" and the "NFI-based model" was just 1%, never exceeding 2% in any region (Figure 7D). Across the 86 subregions, the mean absolute difference was 2%, with only two subregions exceeding 5% (Figure 7E). At the NFI plot scale, although discrepancies remained substantial, they were markedly reduced: differences approximated 10% for around one-third of plots (compared to 60% of the plots when using the average coefficient) and exceeded 20% for about 9% of plots (versus 25% of the plots when

480 using the average coefficient; (Figure 7F). Thus, despite the systematic bias observed at the species level (Figure 5), the "GIS-based model" contributes meaningfully to accounting for wood density variation from regional to local scales.

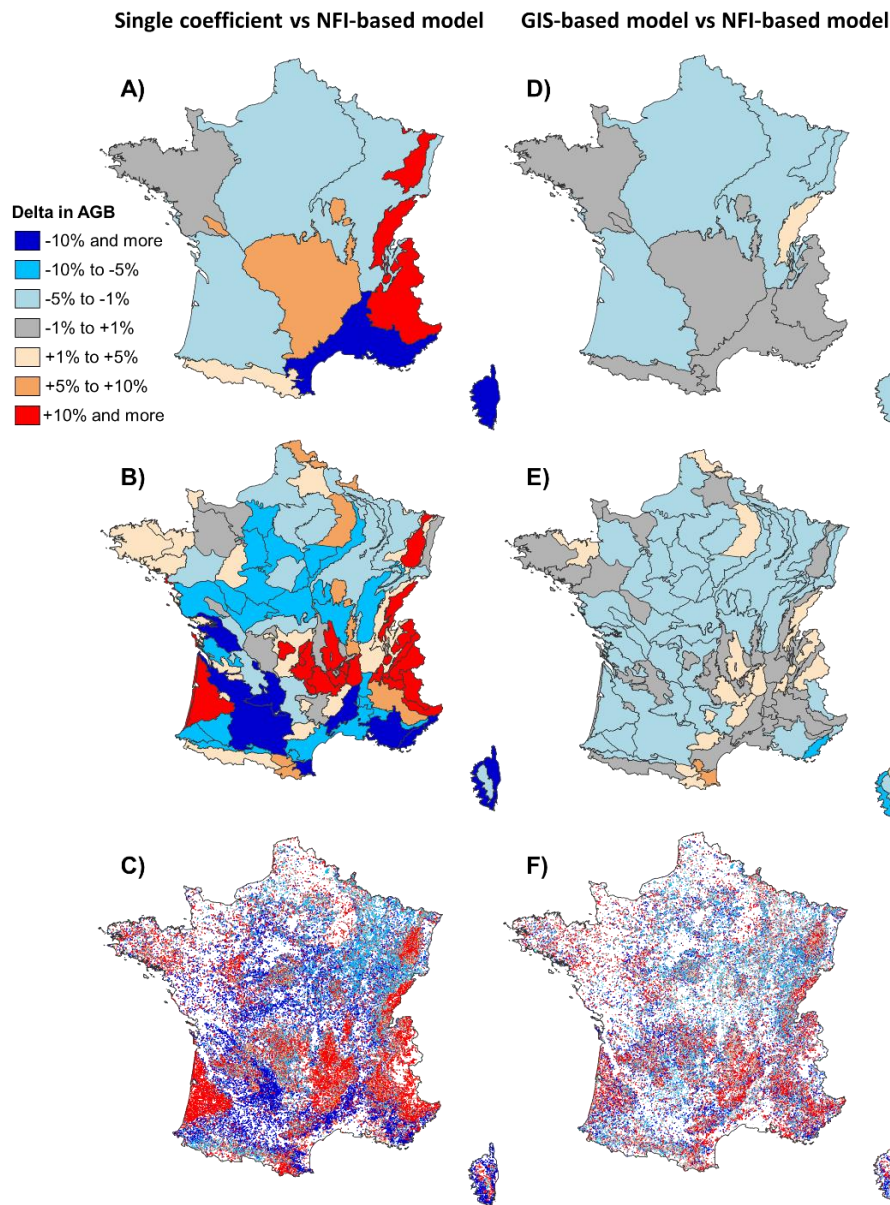



Figure 7: Difference in forest aboveground biomass (AGB) stock depending on the method used to predict wood density: the "NFI-based model", the "GIS-based model" or a single average coefficient. Comparisons are presented across three spatial levels: biogeographical regions (A and D), biogeographical subregions (B and E), and forest plots inventoried by the French NFI (C and F). Maps on the left show the difference in AGB between estimates derived from the "NFI-based model" and those using the average coefficient. Maps on the right display the difference between estimates derived from the "GIS-based model" and "NFI-based model". All differences are expressed relative to the AGB estimated using the "NFI-based model".

4 Discussion

4.1 Characterising wood density variation in temperate forests

This study, based on a large dataset of wood density measurements collected using a standardised protocol across France, provides a comprehensive characterisation of variation in wood density at both interspecific and intraspecific levels across
495 temperate forests. Our findings reveal substantial variability between species—78.5% of the total variance—but also within them, resulting in pronounced spatial patterns in the distribution of wood density.

Across the dataset, wood density values ranged from approximately 300 to 900 kg·m⁻³, varying by a factor of two to three both within and between species. These patterns align with those observed in the *GenTree* dataset, which covers a broader European
500 range, although based on fewer individual trees and species (Martínez-Sancho et al., 2020; see Cuny et al., 2025 for comparison of the two datasets).

4.2 The diversity in wood density observed in temperate French forests is comparable to that observed worldwide

While recent studies have primarily examined interspecific variation in wood density at the global scale (Mo et al., 2024; Yang et al., 2024) or within tropical forests (Phillips et al., 2019; Sullivan et al., 2025), our study highlights that temperate forests
505 exhibit a degree of wood density variability comparable to their tropical counterparts, despite their lower species richness. Tropical species typically show mean wood density values between 300 and 900 kg m⁻³ (Lewis et al., 2013; Phillips et al., 2019; Reyes et al., 1992), with a pantropical mean of 619 kg m⁻³ In comparison, we found species-specific averages spanning from 380 to 850 kg m⁻³ and a mean value of 575 kg m⁻³ for French forests.

510 Intraspecific variation was also substantial. For instance, *Quercus petraea* exhibited wood density values ranging from approximately 400 to 900 kg m⁻³ in France—comparable to the full range observed across tropical zones. Moreover, intra-tree variation (e.g. from pith to bark, base to crown, or between stem and branches) can equal or exceed inter-individual variation within a species (Billard et al., 2021; Bouriaud et al., 2015; Franceschini et al., 2010, 2013).

4.3 What are the drivers of variation in wood density in temperate forests?

515 Recent global studies have shown that tree species and hydrothermal conditions (regional temperature and precipitation) are key drivers of wood density variation (Mo et al., 2024; Yang et al., 2024). Our results, based on more intensive sampling at a national scale, confirm that species composition is the dominant factor in temperate forests (Kerfriden et al., 2021), explaining nearly 80% of the observed variation in wood density—similar to findings in tropical systems (Farias et al., 2023). While mean annual temperature did emerge as a significant predictor, its effect was moderate.

520

Environmental factors can indirectly influence wood density through species composition, tree dimensions, or stand characteristics. As a result, their effects may be partially captured by variables representing these features. For instance, tree-ring width is known to respond strongly to climatic conditions (George, 2014), and in turn, can significantly influence wood density (Guilley et al., 2004; Saranpää, 2003; Zobel and van Buijtenen, 1989). Including tree-ring width as a covariate in statistical models can therefore reduce the apparent influence of environmental variables on wood density, as it acts as a mediating factor (Bergès et al., 2008). Even so, when tree- and stand-level variables were excluded in favour of purely environmental predictors within the "environmental model", the proportion of wood density variance explained by temperature and precipitation remained low, indicating that climatic conditions alone account for a limited share of the overall variation at this spatial scale. Mean annual temperature, however, showed a strong positive effect on wood density variation, both within species (even when tree-ring width was controlled for) and across the entire dataset.

This discrepancy with more global studies can likely be attributed to the spatial scale of analysis. At the global level, climatic gradients play a dominant role in shaping tree species distributions, from low wood density coniferous species in boreal forests to high wood density broadleaf species in tropical forests. In contrast, within a country like France, species distribution is also strongly influenced by silvicultural practices, which can uncouple species composition from local climatic conditions (Bontemps et al., 2019). As a result, the indirect effect of regional variation in climate conditions on wood density—via their influence on species composition—is likely more limited at this scale.

Regarding intraspecific variation in wood density, we found that variables related to tree size and growth rate (as estimated by the average width of the last five tree-rings) were the most important. The direction of the relationship between growth and wood density was consistent with known wood anatomical patterns. In ring-porous broadleaves (e.g. *Quercus*, *Fraxinus*), wider rings tend to contain more latewood, resulting in higher density. In contrast, in conifers, wider rings typically contain a greater proportion of earlywood, leading to lower density (Lachenbruch et al., 2011; Zobel and van Buijtenen, 1989). Our models reflected these patterns: we observed positive effects of ring width on wood density in ring-porous species, negative effects in conifers, and species-specific responses in diffuse- or semi-ring-porous species (e.g. positive in *Fagus sylvatica*, negative in *Betula pendula*), in line with previous findings (Lachenbruch et al., 2011).

The effect of tree diameter, identified as the third most influential predictor in the "NFI-based model" (Figure 2), also merits attention due to its quasi-systematic positive association with wood density. Since tree volume and various mechanical properties scale as power functions of tree size (King, 1990), this trend likely reflects mechanical constraints inherent to tree growth. Moreover, the relationship may have practical relevance in forest ecosystems undergoing maturation (Bontemps et al., 2020).

4.4 Why intraspecific variation in wood density remains hard to capture

Despite consistent relationships with covariates, our models captured only a small part of the intraspecific variation in wood density. Several hypotheses may account for this.

555

First, average wood density—whether at the tree-ring or stem level—is known to be a relatively conserved trait under strong developmental control (Cuny and Rathgeber, 2016; Siefert et al., 2015; Swenson and Enquist, 2007), with high heritability and substantial additive genetic effects (Gaspar et al., 2008; Montes and Weber, 2009; Rozenberg et al., 2001; Soro et al., 2023). Even though growth traits such as ring width and stem size are correlated with wood density, they typically explain

560 only a limited portion of its variation (Bouriaud et al., 2004). The remaining unexplained variance is often captured as a "tree effect" in statistical models, reflecting individual-level differences not accounted for by measured predictors (Bontemps et al., 2013; Franceschini et al., 2012; Guilley et al., 2004). Given the significance of this residual variability, advancing genetic mapping of tree populations and their diversity may offer a promising avenue for deeper insight (Porth and El-Kassaby, 2014), NFI providing an ideal framework for integrating such complementary measurements.

565

Second, certain potentially influential predictors (e.g., tree age and average tree-ring width) were excluded from the main analysis, as they were available only for a subset of trees (Cuny et al., 2025). However, when using this subset, incorporating these variables only led to a modest improvement in the performance of the "NFI-based model", with an additional 1% of captured intraspecific variation.

570

Finally, we investigated whether the limited explanatory power of our models could stem from the modelling approach itself. This hypothesis was first challenged by the comparison of model performance on train and test datasets, which revealed remarkably similar results (Table 2). To further assess this, we implemented an additional random forest model using the *ranger* package in R (Wright and Ziegler, 2017), capable of capturing nonlinear relationships and interactions. Using the same

575 set of predictors as in the "NFI-based model", the random forest model yielded comparable predictive accuracy, with a mean absolute error of 36 kg m^{-3} and an R² of 0.82 on both train and test datasets (Supplementary Figure S6). These findings suggest that linear models, despite their simplicity, are well suited to this type of analysis and remain appropriate for predictive applications, offering the added benefit of interpretability

4.5 What method should be used to infer wood density for forest biomass and carbon assessments? Scale matters

580 Our results show that the importance of the method chosen to infer wood density and ultimately calculate AGB depends largely on the spatial scale. At broad spatial scales (e.g., national forest biomass assessments), the choice of the method to infer wood density has little impact. Even simplified assumptions, such as using a single average wood density value, produced results consistent with those from more detailed models. However, it is important to note that the average coefficient used in this

study was derived from comprehensive systematic sampling and weighted by species' contributions to total growing stock. As such, it is highly representative of French forests. Coefficients derived from other, less comprehensive datasets may lead to lower predictive performances.

At finer spatial scales, our findings demonstrate that using coarse coefficients that ignore wood density variability can introduce significant biases in forest biomass estimates. Paradoxically, detailed species-specific coefficients tend to be used at broad scales, while spatialised biomass and carbon estimates—particularly those derived from remote sensing—tend to rely on models that poorly account for wood density variation (Liu et al., 2023; Ma et al., 2024; Schwartz et al., 2023; Yang et al., 2022). These remote sensing techniques offer great potential for biomass mapping, as they can allow the estimation of tree volume and biomass from canopy height. However, currently available remote sensing products do not permit to identify tree species, which prevents to incorporate wood density in the derived estimations. As a result, coarse approximations are typically used to convert volume into biomass, which can lead to substantial biases compared to ground-based estimates (Phillips et al., 2019; Sæbø et al., 2022).

Our analyses indicate that detailed, tree-level data are essential for accurately modelling wood density variation. Using climatic variables and general stand-level descriptors only partially capture this variability. Nonetheless, our "GIS-based model" demonstrated that incorporating such descriptors improves estimates of forest biomass and carbon stocks, even at fine spatial scales. Given that these variables are—or could be—available as GIS layers, this approach may be suitable for spatially explicit assessments of forest biomass and carbon stocks. Among all variables, stand composition emerged as the most influential factor, reflecting the dominant role of species identity in determining wood density. We relied on the "BD Forêt" database to characterise stand composition. While this map is no longer fully up to date, its revision could enhance the accuracy of wood density estimates by better capturing current species distributions. However, the exclusion of plot-level attributes revealed a clear process of regression toward the mean (Figure 5), particularly concerning for coniferous forests, where the bias is unidirectional. The generality of this effect in GIS-based developments has been shown to have substantial implications for strategic forest planning (Ulvdal et al., 2025).

As a general rule, because tree identity is the primary driver of wood density variation, incorporating species-specific hypotheses on wood density significantly improves biomass estimates. We therefore encourage remote sensing approaches to integrate interspecific variability wherever possible. This can be achieved either by complementing remote data with ground-based species inventories (Chave et al., 2019) or by leveraging recent advances in species recognition from processed imagery (Effendi et al., 2021; Ma et al., 2024).

4 Conclusions

- This study provides new insights into wood density variation and its underlying drivers in temperate forests.
- Species identity emerged as the dominant factor shaping wood density variation, leading to clear spatial patterns aligned with species distribution. Intraspecific variation was also substantial and influenced by tree size, growth rate, and mean annual temperature—although only partially captured by our models.
- While accounting for wood density variation has limited impact on aboveground biomass estimates at the national scale— provided that representative coefficients are used—it significantly affects estimates at finer spatial resolutions.
- Given the strong influence of tree species and the limited predictability of intraspecific variation, we recommend using detailed species-level average wood density coefficients for forest biomass and carbon stock assessment.
- Considering the well-documented inter-individual variability in wood density, future efforts to characterise the genetic structure of tree populations at broad scales using high-throughput technologies may offer valuable insights, but remain a methodological challenge.

Author contributions

H.C. conducted the research, drew the figures and wrote the manuscript, in close coordination with J.-M.L. and J.-D.B. All authors critically reviewed the manuscript and approved the current version.

Acknowledgements

A.L.S. is funded by the project ALAMOD of the exploratory research program FairCarboN and received government funding managed by the Agence Nationale de la Recherche under the France 2030 program, reference ANR-22-PEXF-0002.

H.C. thanks Claire Bastick for help in integrating the aboveground biomass estimates in the calculation process of the French NFI, and Timothée Nayme for help in calculating stand dominant height.

Conflict of interest statement

Authors declare that they have no competing interests.

References

Armstrong, J. S. and Collopy, F.: Error measures for generalizing about forecasting methods: Empirical comparisons, International journal of forecasting, 8, 69–80, https://doi.org/10.1016/0169-2070(92)90008-W, 1992.

645 Baker, T. R., Phillips, O. L., Malhi, Y., Almeida, S., Arroyo, L., Di Fiore, A., Erwin, T., Killeen, T. J., Laurance, S. G., Laurance, W. F., Lewis, S. L., Lloyd, J., Monteagudo, A., Neill, D. A., Patiño, S., Pitman, N. C. A., M. Silva, J. N., and Vásquez Martínez, R.: Variation in wood density determines spatial patterns in Amazonian forest biomass, Global Change Biology, 10, 545–562, https://doi.org/10.1111/j.1365-2486.2004.00751.x, 2004.

Bergès, L., Nepveu, G., and Franc, A.: Effects of ecological factors on radial growth and wood density components of sessile oak (Quercus petraea Liebl.) in Northern France, Forest Ecology and Management, 255, 567–579, 650 https://doi.org/10.1016/j.foreco.2007.09.027, 2008.

Besic, N., Picard, N., Vega, C., Bontemps, J.-D., Hertzog, L., Renaud, J.-P., Fogel, F., Schwartz, M., Pellissier-Tanon, A., Destouet, G., and others: Remote-sensing-based forest canopy height mapping: some models are useful, but might they provide us with even more insights when combined?, Geoscientific Model Development, 18, 337–359, 2025.

Billard, A., Bauer, R., Mothe, F., Colin, F., Deleuze, C., and Longuetaud, F.: Vertical variations in wood basic density for two 655 softwood species, European Journal of Forest Research, 140, 1401–1416, https://doi.org/10.1007/s10342-021-01402-y, 2021.

Bontemps, J.-D. and Bouriaud, O.: Take five: about the beat and the bar of annual and 5-year periodic national forest inventories, Annals of Forest Science, 81, 53, https://doi.org/10.1186/s13595-024-01268-1, 2024.

Bontemps, J.-D., Gelhaye, P., Nepveu, G., and Hervé, J.-C.: When tree rings behave like foam: moderate historical decrease in the mean ring density of common beech paralleling a strong historical growth increase, Annals of Forest Science, 70, 329–660 343, https://doi.org/10.1007/s13595-013-0263-2, 2013.

Bontemps, J.-D., Hervé, J.-C., and Denardou, A.: Partition idéalisée et régionalisée de la composition en espèces ligneuses des forêts françaises, Écoscience, 26, 291–308, https://doi.org/10.1080/11956860.2019.1588511, 2019.

Bontemps, J.-D., Denardou, A., Hervé, J.-C., Bir, J., and Dupouey, J.-L.: Unprecedented pluri-decennial increase in the growing stock of French forests is persistent and dominated by private broadleaved forests, Annals of Forest Science, 77, 1–665 20, https://doi.org/10.1007/s13595-020-01003-6, 2020.

Bouriaud, O., Bréda, N., Le Moguedec, G., and Nepveu, G.: Modelling variability of wood density in beech as affected by ring age, radial growth and climate, Trees, 18, 264–276, https://doi.org/10.1007/s00468-003-0303-x, 2004.

Bouriaud, O., Teodosiu, M., Kirdyanov, A., and Wirth, C.: Influence of wood density in tree-ring-based annual productivity assessments and its errors in Norway spruce, Biogeosciences, 12, 6205–6217, https://doi.org/10.5194/bg-12-6205-2015, 2015.

670 Bouriaud, O., Morneau, F., and Bontemps, J.-D.: Square-grid sampling support to reconcile systematicity and adaptivity in periodic spatial surveys of natural populations, Journal of Vegetation Science, 34, e13195, https://doi.org/10.1111/jvs.13195, 2023.

Briffa, K. R., Jones, P. D., Schweingruber, F. H., and Osborn, T. J.: Influence of volcanic eruptions on Northern Hemisphere summer temperature over the past 600 years, Nature, 393, 450–455, https://doi.org/10.1038/30943, 1998.

675 Canellas, C., Gibelin, A.-L., Lassègues, P., Kerdoncuff, M., Dandin, P., and Simon, P.: Les normales climatiques spatialisées Aurelhy 1981-2010: températures et précipitations, La météorologie, 2014, 47–55, https://doi.org/10.4267/2042/53750, 2014.

Cavaignac, S.: Les sylvoécorégions (SER) de France métropolitaine, Etude de définition, Report, French National Forest Inventory, Nogent-sur-Vernisson, 2009.

680   Chave, J., Condit, R., Aguilar, S., Hernandez, A., Lao, S., and Perez, R.: Error propagation and scaling for tropical forest biomass estimates, Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences, 359, 409–420, https://doi.org/10.1093/acprof:oso/9780198567066.003.0013, 2004.

Chave, J., Muller-Landau, H. C., Baker, T. R., Easdale, T. A., Steege, H. ter, and Webb, C. O.: Regional and phylogenetic variation of wood density across 2456 neotropical tree species, Ecological applications, 16, 2356–2367, https://doi.org/10.1890/1051-0761(2006)016[2356:RAPVOW]2.0.CO;2, 2006.

685   Chave, J., Coomes, D., Jansen, S., Lewis, S. L., Swenson, N. G., and Zanne, A. E.: Towards a worldwide wood economics spectrum, Ecology Letters, 12, 351–366, https://doi.org/10.1111/j.1461-0248.2009.01285.x, 2009.

Chave, J., Davies, S. J., Phillips, O. L., Lewis, S. L., Sist, P., Schepaschenko, D., Armston, J., Baker, T. R., Coomes, D., Disney, M., and others: Ground data are essential for biomass remote sensing missions, Surveys in Geophysics, 40, 863–880, https://doi.org/10.1007/s10712-019-09528-w, 2019.

690   Cuny, H., Leban, J.-M., Hervé, J.-C., Bontemps, J.-D., Kerfriden, B., Jacquin, P., Lacarin, M., Dauffy, V., Duprez, C., and Wurpillot, S.: XyloDensMap: a georeferenced dataset for the wood density of 110,000 trees from 156 European species in France, https://doi.org/10.6084/m9.figshare.c.7515396, 2024.

Cuny, H., Leban, J.-M., Hervé, J.-C., Bontemps, J.-D., Kerfriden, B., Jacquin, P., Lacarin, M., Dauffy, V., Duprez, C., and Wurpillot, S.: XyloDensMap: a georeferenced dataset for the wood density of 110,000 trees from 156 European species in
695   France, Scientific Data, 12, 380, https://doi.org/10.1038/s41597-025-04645-1, 2025.

Cuny, H. E. and Rathgeber, C. B.: Xylogenesis: coniferous trees of temperate forests are listening to the climate tale during the growing season but only remember the last words!, Plant physiology, 171, 306–317, https://doi.org/10.1104/pp.16.00037, 2016.

Dalla-Salda, G., Martinez-Meier, A., Cochard, H., and Rozenberg, P.: Variation of wood density and hydraulic properties of
700   Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) clones related to a heat and drought wave in France, Forest Ecology and Management, 257, 182–189, https://doi.org/10.1016/j.foreco.2008.08.019, 2009.

Doraisami, M., Domke, G. M., and Martin, A. R.: Improving wood carbon fractions for multiscale forest carbon estimation, Carbon Balance and Management, 19, 25, https://doi.org/10.1186/s13021-024-00272-2, 2024.

Effendi, N. A. F. N., Zaki, N. A. M., Latif, Z. A., Suratman, M. N., Bohari, S. N., Zainal, M. Z., and and, H. O.: Unlocking
705   the potential of hyperspectral and LiDAR for above-ground biomass (AGB) and tree species classification in tropical forests, Geocarto International, 37, 8036–8061, https://doi.org/10.1080/10106049.2021.1990419, 2021.

Eggleston, H., Buendia, L., Miwa, K., Ngara, T., and Tanabe, K.: 2006 IPCC guidelines for national greenhouse gas inventories, 2006.

Fajardo, A.: Wood density is a poor predictor of competitive ability among individuals of the same species, Forest Ecology
710   and Management, 372, 217–225, https://doi.org/10.1016/j.foreco.2016.04.022, 2016.

Fajardo, A., Siefert, A., and Laughlin, D. C.: Wood density and leaf size jointly predict woody plant growth rates across (but not within) species along a steep precipitation gradient, Journal of Ecology, 112, 374–388, https://doi.org/10.1111/1365-2745.14240, 2024.

Farias, H. L. S., Pequeno, P. A. C. L., Silva, W. R., Melo, V. F., Carvalho, L. C. D. S., Perdiz, R. D. O., Citó, A. C., Fearnside, P. M., and Barbosa, R. I.: Amazon forest biomass: intra-and interspecific variability in wood density drive divergences in Brazil's far north, iForest-Biogeosciences and Forestry, 16, 95, https://doi.org/10.3832/ifor4137-016, 2023.

Flores, O. and Coomes, D. A.: Estimating the wood density of species for carbon stock assessments, Methods in Ecology and Evolution, 2, 214–220, https://doi.org/10.1111/j.2041-210X.2010.00068.x, 2011.

Fox, J. and Weisberg, S.: An R Companion to Applied Regression, Third., Sage, Thousand Oaks CA, 2019.

Franceschini, T., Bontemps, J.-D., Gelhaye, P., Rittie, D., Herve, J.-C., Gegout, J.-C., and Leban, J.-M.: Decreasing trend and fluctuations in the mean ring density of Norway spruce through the twentieth century, Ann. For. Sci., 67, 816–816, https://doi.org/10.1051/forest/2010055, 2010.

Franceschini, T., Bontemps, J.-D., and Leban, J.-M.: Transient historical decrease in earlywood and latewood density and unstable sensitivity to summer temperature for Norway spruce in northeastern France, Canadian Journal of Forest Research, 42, 219–226, https://doi.org/10.1139/x11-182, 2012.

Franceschini, T., Longuetaud, F., Bontemps, J.-D., Bouriaud, O., Caritey, B.-D., and Leban, J.-M.: Effect of ring width, cambial age, and climatic variables on the within-ring wood density profile of Norway spruce Picea abies (L.) Karst., Trees, 27, 913–925, https://doi.org/10.1007/s00468-013-0844-6, 2013.

Freyburger, C., Longuetaud, F., Mothe, F., Constant, T., and Leban, J.-M.: Measuring wood density by means of X-ray computer tomography, Ann. For. Sci., 66, 804–804, https://doi.org/10.1051/forest/2009071, 2009.

Friedlingstein, P., O'Sullivan, M., Jones, M. W., Andrew, R. M., Bakker, D. C. E., Hauck, J., Landschützer, P., Le Quéré, C., Luijkx, I. T., Peters, G. P., Peters, W., Pongratz, J., Schwingshackl, C., Sitch, S., Canadell, J. G., Ciais, P., Jackson, R. B., Alin, S. R., Anthoni, P., Barbero, L., Bates, N. R., Becker, M., Bellouin, N., Decharme, B., Bopp, L., Brasika, I. B. M., Cadule, P., Chamberlain, M. A., Chandra, N., Chau, T.-T.-T., Chevallier, F., Chini, L. P., Cronin, M., Dou, X., Enyo, K., Evans, W., Falk, S., Feely, R. A., Feng, L., Ford, D. J., Gasser, T., Ghattas, J., Gkritzalis, T., Grassi, G., Gregor, L., Gruber, N., Gürses, Ö., Harris, I., Hefner, M., Heinke, J., Houghton, R. A., Hurtt, G. C., Iida, Y., Ilyina, T., Jacobson, A. R., Jain, A., Jarníková, T., Jersild, A., Jiang, F., Jin, Z., Joos, F., Kato, E., Keeling, R. F., Kennedy, D., Klein Goldewijk, K., Knauer, J., Korsbakken, J. I., Körtzinger, A., Lan, X., Lefèvre, N., Li, H., Liu, J., Liu, Z., Ma, L., Marland, G., Mayot, N., McGuire, P. C., McKinley, G. A., Meyer, G., Morgan, E. J., Munro, D. R., Nakaoka, S.-I., Niwa, Y., O'Brien, K. M., Olsen, A., Omar, A. M., Ono, T., Paulsen, M., Pierrot, D., Pocock, K., Poulter, B., Powis, C. M., Rehder, G., Resplandy, L., Robertson, E., Rödenbeck, C., Rosan, T. M., Schwinger, J., Séférian, R., et al.: Global Carbon Budget 2023, Earth Syst. Sci. Data, 15, 5301–5369, https://doi.org/10.5194/essd-15-5301-2023, 2023.

Gaspar, M. J., Louzada, J. L., Aguiar, A., and Almeida, M. H.: Genetic correlations between wood quality traits of Pinus pinaster Ait., Annals of Forest Science, 65, 1, https://doi.org/10.1051/forest:2008054, 2008.

George, S. S.: An overview of tree-ring width records across the Northern Hemisphere, Quaternary Science Reviews, 95, 132–150, https://doi.org/10.1016/j.quascirev.2014.04.029, 2014.

Groemping, U.: Relative Importance for Linear Regression in R: The Package relaimpo, Journal of Statistical Software, 17, 1–27, https://doi.org/10.18637/jss.v017.i01, 2006.

Groombridge, B. and Jenkins, M. D.: World Atlas of Biodiversity: Earth's Living Resources in the 21st Century, University of California Press, California, USA, 340 pp., 2002.

Guilley, E., Hervé, J.-C., and Nepveu, G.: The influence of site quality, silviculture and region on wood density mixed model in Quercus petraea Liebl., Forest Ecology and Management, 189, 111–121, https://doi.org/10.1016/j.foreco.2003.07.033, 2004.

Houllier, F., Leban, J.-M., and Colin, F.: Linking growth modelling to timber quality assessment for Norway spruce, Forest Ecology and Management, 74, 91–102, https://doi.org/10.1016/0378-1127(94)03510-4, 1995.

Hughes, M., Schweingruber, F., Cartwright, D., and Kelly, P.: July–August temperature at Edinburgh between 1721 and 1975 from tree-ring density and width data, Nature, 308, 341–344, https://doi.org/10.1038/308341a0, 1984.

Jacquin, P., Mothe, F., Longuetaud, F., Billard, A., Kerfriden, B., and Leban, J.-M.: CarDen: A software for fast measurement of wood density on increment cores by CT scanning, Computers and Electronics in Agriculture, 156, 606–617, https://doi.org/10.1016/j.compag.2018.12.008, 2019.

Jenkins, J. C., Chojnacky, D. C., Heath, L. S., and Birdsey, R. A.: National scale biomass estimators for United States tree species, Forest Science. 49: 12-35, https://doi.org/10.1093/forestscience/49.1.12, 2003.

Kattge, J., Bönisch, G., Díaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Tautenhahn, S., Werner, G. D. A., Aakala, T., Abedi, M., Acosta, A. T. R., Adamidis, G. C., Adamson, K., Aiba, M., Albert, C. H., Alcántara, J. M., Alcázar C, C., Aleixo, I., Ali, H., Amiaud, B., Ammer, C., Amoroso, M. M., Anand, M., Anderson, C., Anten, N., Antos, J., Apgaua, D. M. G., Ashman, T.-L., Asmara, D. H., Asner, G. P., Aspinwall, M., Atkin, O., Aubin, I., Baastrup-Spohr, L., Bahalkeh, K., Bahn, M., Baker, T., Baker, W. J., Bakker, J. P., Baldocchi, D., Baltzer, J., Banerjee, A., Baranger, A., Barlow, J., Barneche, D. R., Baruch, Z., Bastianelli, D., Battles, J., Bauerle, W., Bauters, M., Bazzato, E., Beckmann, M., Beeckman, H., Beierkuhnlein, C., Bekker, R., Belfry, G., Belluau, M., Beloiu, M., Benavides, R., Benomar, L., Berdugo-Lattke, M. L., Berenguer, E., Bergamin, R., Bergmann, J., Bergmann Carlucci, M., Berner, L., Bernhardt-Römermann, M., Bigler, C., Bjorkman, A. D., Blackman, C., Blanco, C., Blonder, B., Blumenthal, D., Bocanegra-González, K. T., Boeckx, P., Bohlman, S., Böhning-Gaese, K., Boisvert-Marsh, L., Bond, W., Bond-Lamberty, B., Boom, A., Boonman, C. C. F., Bordin, K., Boughton, E. H., Boukili, V., Bowman, D. M. J. S., Bravo, S., Brendel, M. R., Broadley, M. R., Brown, K. A., Bruelheide, H., Brumnich, F., Bruun, H. H., Bruy, D., Buchanan, S. W., Bucher, S. F., Buchmann, N., Buitenwerf, R., Bunker, D. E., et al.: TRY plant trait database - enhanced coverage and open access, Glob Chang Biol, 26, 119–188, https://doi.org/10.1111/gcb.14904, 2020.

Kerfriden, B., Bontemps, J.-D., and Leban, J.-M.: Variations in temperate forest stem biomass ratio along three environmental gradients are dominated by interspecific differences in wood density, Plant Ecol, 222, 289–303, https://doi.org/10.1007/s11258-020-01106-0, 2021.

King, D. A.: The adaptive significance of tree height, The American Naturalist, 135, 809–828, https://doi.org/10.1086/285075, 1990.

Kuhn and Max: Building Predictive Models in R Using the caret Package, Journal of Statistical Software, 28, 1–26, https://doi.org/10.18637/jss.v028.i05, 2008.

Labrière, N., Davies, S. J., Disney, M. I., Duncanson, L. I., Herold, M., Lewis, S. L., Phillips, O. L., Quegan, S., Saatchi, S. S., Schepaschenko, D. G., and others: Toward a forest biomass reference measurement system for remote sensing applications, Global Change Biology, 29, 827–840, https://doi.org/10.1111/gcb.16497, 2023.

Lachenbruch, B., Moore, J. R., and Evans, R.: Radial Variation in Wood Structure and Function in Woody Plants, and Hypotheses for Its Occurrence, in: Size- and Age-Related Changes in Tree Structure and Function, edited by: Meinzer, F. C., Lachenbruch, B., and Dawson, T. E., Springer Netherlands, Dordrecht, 121–164, https://doi.org/10.1007/978-94-007-1242-3_5, 2011.

790 Lewis, S., Sonké, B., Sunderland, T., Begne, S., Lopez-Gonzalez, G., van der Heijden, G., Phillips, O., Affum-Baffoe, K., Baker, T., Banin, L., and others: Above-ground biomass and structure of 260 African tropical forests, Philos, TR Soc. B, 368, 20120295, https://doi. org/10.1098/rstb, 2013.

Li, F., Qian, H., Sardans, J., Amishev, D. Y., Wang, Z., Zhang, C., Wu, T., Xu, X., Tao, X., and Huang, X.: Evolutionary history shapes variation of wood density of tree species across the world, Plant Diversity, 46, 283–293, https://doi.org/10.1016/j.pld.2024.04.002, 2024.

Liu, S., Brandt, M., Nord-Larsen, T., Chave, J., Reiner, F., Lang, N., Tong, X., Ciais, P., Igel, C., Pascual, A., and others: The overlooked contribution of trees outside forests to tree cover and woody biomass across Europe, Science Advances, 9, eadh4097, https://doi.org/10.1126/sciadv.adh4097, 2023.

Loustau, D.: Projet CARBOFOR : Séquestration de Carbone dans les grands écosystèmes forestiers en France. Quantification, spatialisation, vulnérabilité et impacts de différents scénarios climatiques et sylvicoles., 2002.

Ma, T., Zhang, C., Ji, L., Zuo, Z., Beckline, M., Hu, Y., Li, X., and Xiao, X.: Development of forest aboveground biomass estimation, its problems and future solutions: A review, Ecological Indicators, 159, 111653, https://doi.org/10.1016/j.ecolind.2024.111653, 2024.

Martin-Ducup, O., Dupuy, J.-L., Soma, M., Guerra-Hernandez, J., Marino, E., Fernandes, P. M., Just, A., Corbera, J., Toutchkov, M., Sorribas, C., and others: Unlocking the potential of Airborne LiDAR for direct assessment of fuel bulk density and load distributions for wildfire hazard mapping, Agricultural and Forest Meteorology, 362, 110341, https://doi.org/10.1016/j.agrformet.2024.110341, 2025.

Martínez-Sancho, E., Slámová, L., Morganti, S., Grefen, C., Carvalho, B., Dauphin, B., Rellstab, C., Gugerli, F., Opgenoorth, L., Heer, K., Knutzen, F., von Arx, G., Valladares, F., Cavers, S., Fady, B., Alía, R., Aravanopoulos, F., Avanzi, C., Bagnoli, F., Barbas, E., Bastien, C., Benavides, R., Bernier, F., Bodineau, G., Bastias, C. C., Charpentier, J.-P., Climent, J. M., Corréard, M., Courdier, F., Danusevicius, D., Farsakoglou, A.-M., del Barrio, J. M. G., Gilg, O., González-Martínez, S. C., Gray, A., Hartleitner, C., Hurel, A., Jouineau, A., Kärkkäinen, K., Kujala, S. T., Labriola, M., Lascoux, M., Lefebvre, M., Lejeune, V., Le-Provost, G., Liesebach, M., Malliarou, E., Mariotte, N., Matesanz, S., Michotey, C., Milesi, P., Myking, T., Notivol, E., Pakull, B., Piotti, A., Plomion, C., Pringarbe, M., Pyhäjärvi, T., Raffin, A., Ramírez-Valiente, J. A., Ramskogler, K., Robledo-Arnuncio, J. J., Savolainen, O., Schueler, S., Semerikov, V., Spanu, I., Thévenet, J., Mette Tollefsrud, M., Turion, N., Veisse, D., Vendramin, G. G., Villar, M., Westin, J., and Fonti, P.: The GenTree Dendroecological Collection, tree-ring and wood density data from seven tree species across Europe, Sci Data, 7, 1, https://doi.org/10.1038/s41597-019-0340-y, 2020.

Mathieu, A.: Description des bois des essences forestières les plus importantes., Grimblot et veuve Raybois, Nancy, 1855.

Mayer, D. and Butler, D.: Statistical validation, Ecological modelling, 68, 21–32, https://doi.org/10.1016/0304-3800(93)90105-2, 1993.

Mo, L., Crowther, T. W., Maynard, D. S., Van den Hoogen, J., Ma, H., Bialic-Murphy, L., Liang, J., De-Miguel, S., Nabuurs, G.-J., Reich, P. B., and others: The global distribution and drivers of wood density and their impact on forest carbon stocks, Nature Ecology & Evolution, 1–18, https://doi.org/10.1038/s41559-024-02564-9, 2024.

Montes, C. S. and Weber, J. C.: Genetic variation in wood density and correlations with tree growth in Prosopis africana from Burkina Faso and Niger, Annals of Forest Science, 66, 1–9, https://doi.org/10.1051/forest/2009060, 2009.

Nascimento, H. E. M., Laurance, W. F., Condit, R., Laurance, S. G., D'Angelo, S., and Andrade, A. C.: Demographic and life-history correlates for Amazonian trees, Journal of Vegetation Science, 16, 625–634, https://doi.org/10.1111/j.1654-1103.2005.tb02405.x, 2005.

Pan, Y., Birdsey, R. A., Phillips, O. L., Houghton, R. A., Fang, J., Kauppi, P. E., Keith, H., Kurz, W. A., Ito, A., and Lewis,
830   S. L.: The enduring world forest carbon sink, Nature, 631, 563–569, https://doi.org/10.1038/s41586-024-07602-x, 2024.

Pellissier-Tanon, A., Ciais, P., Schwartz, M., Fayad, I., Xu, Y., Ritter, F., De Truchis, A., and Leban, J.-M.: Combining satellite
images with national forest inventory measurements for monitoring post-disturbance forest height growth, Frontiers in Remote
Sensing, 5, 1432577, https://doi.org/10.3389/frsen.2024.1432577, 2024.

Penman, J., Gytarsky, M., Hiraishi, T., Krug, T., Kruger, D., Pipatti, R., Buendia, L., Miwa, K., Ngara, T., Tanabe, K., and
835   others: Good practice guidance for land use, land-use change and forestry, 2003.

Phillips, O. L., Sullivan, M. J. P., Baker, T. R., Monteagudo Mendoza, A., Vargas, P. N., and Vásquez, R.: Species Matter:
Wood Density Influences Tropical Forest Biomass at Multiple Scales, Surv Geophys, 40, 913–935,
https://doi.org/10.1007/s10712-019-09540-0, 2019.

Porth, I. and El-Kassaby, Y. A.: Assessment of the genetic diversity in forest tree populations using molecular markers,
840   Diversity, 6, 283–295, https://doi.org/10.3390/d6020283, 2014.

R Core Team: R: A Language and Environment for Statistical Computing, 2023.

Reyes, G., Brown, S., Chapman, J., and Lugo, A.: Wood densities of tropical tree species, US Department of Agriculture,
Forest Service, Southern Forest Experiment Station, New Orleans, LA, 1992.

Rozenberg, P., Franc, A., Bastien, C., and Cahalan, C.: Improving models of wood density by including genetic effects: a case
845   study in Douglas-fir, Annals of forest science, 58, 385–394, https://doi.org/10.1051/forest:2001132, 2001.

Sæbø, J. S., Socolar, J. B., Sánchez, E. P., Woodcock, P., Bousfield, C. G., Uribe, C. A. M., Edwards, D. P., and Haugaasen,
T.: Ignoring variation in wood density drives substantial bias in biomass estimates across spatial scales, Environ. Res. Lett.,
17, 054002, https://doi.org/10.1088/1748-9326/ac62ae, 2022.

Santoro, M. and Cartus, O.: ESA Biomass Climate Change Initiative (Biomass_cci): Global datasets of forest above-ground
850   biomass for the years 2010, 2015, 2016, 2017, 2018, 2019, 2020 and 2021, v5. NERC EDS Centre for Environmental Data
Analysis, https://dx.doi.org/10.5285/02e1b18071ad45a19b4d3e8adafa2817, 2024.

Saranpää, P.: Wood density and growth, in: Wood Quality and its Biological Basis, edited by: Barnett, J. R. and Jeronimidis,
G., Blackwell Publishing, CRC Press LLC, 2003.

Schwartz, M., Ciais, P., De Truchis, A., Chave, J., Ottlé, C., Vega, C., Wigneron, J.-P., Nicolas, M., Jouaber, S., Liu, S., and
855   others: FORMS: Forest Multiple Source height, wood volume, and biomass maps in France at 10 to 30 m resolution based on
Sentinel-1, Sentinel-2, and Global Ecosystem Dynamics Investigation (GEDI) data with a deep learning approach, Earth
System Science Data, 15, 4927–4945, https://doi.org/10.5194/essd-15-4927-2023, 2023.

Siefert, A., Violle, C., Chalmandrier, L., Albert, C. H., Taudiere, A., Fajardo, A., Aarssen, L. W., Baraloto, C., Carlucci, M.
B., Cianciaruso, M. V., and others: A global meta-analysis of the relative extent of intraspecific trait variation in plant
860   communities, Ecology letters, 18, 1406–1419, https://doi.org/10.1111/ele.12508, 2015.

Soro, A., Lenz, P., Roussel, J.-R., Larochelle, F., Bousquet, J., and Achim, A.: The phenotypic and genetic effects of drought-
induced stress on apical growth, ring width, wood density and biomass in white spruce seedlings, New Forests, 54, 789–811,
https://doi.org/10.1007/s11056-022-09939-5, 2023.

Su, Y., Schwartz, M., Fayad, I., García, M., Zavala, M. A., Tijerín-Triviño, J., Astigarraga, J., Cruz-Alonso, V., Liu, S., Zhang, X., and others: Canopy height and biomass distribution across the forests of Iberian Peninsula, Scientific Data, 12, 678, 2025.

Sullivan, M. J., Phillips, O. L., Galbraith, D., Almeida, E., de Oliveira, E. A., Almeida, J., Dávila, E. Á., Alves, L. F., Andrade, A., Aragão, L., and others: Variation in wood density across South American tropical forests, Nature Communications, 16, 2351, https://doi.org/10.1038/s41467-025-56175-4, 2025.

Swenson, N. G. and Enquist, B. J.: Ecological and evolutionary determinants of a key plant functional trait: wood density and its community-wide variation across latitude and elevation, American journal of botany, 94, 451–459, https://doi.org/10.3732/ajb.94.3.451, 2007.

Ulvdal, P., Ståhl, G., Sängstuvall, L., Eriksson, O., and Öhman, K.: Long-term strategic forest planning based on biased remote sensing predictions, Forests Monitor, 2, https://doi.org/10.62320/fm.v2i1.25, 2025.

Vallet, P., Dhôte, J.-F., Le Moguédec, G., Ravart, M., and Pignard, G.: Development of total aboveground volume equations for seven important forest tree species in France, Forest Ecology and Management, 229, 98–110, https://doi.org/10.1016/j.foreco.2006.03.013, 2006.

Williamson, G. B. and Wiemann, M. C.: Measuring wood specific gravity…Correctly, American Journal of Botany, 97, 519–524, https://doi.org/10.3732/ajb.0900243, 2010.

Willmott, C. J. and Matsuura, K.: Advantages of the mean absolute error (MAE) over the root mean square error (RMSE) in assessing average model performance, Climate research, 30, 79–82, https://doi.org/10.3354/cr030079, 2005.

Wright, M. N. and Ziegler, A.: ranger: A Fast Implementation of Random Forests for High Dimensional Data in C++ and R, Journal of Statistical Software, 77, 1–17, https://doi.org/10.18637/jss.v077.i01, 2017.

Yang, H., Wang, S., Son, R., Lee, H., Benson, V., Zhang, W., Zhang, Y., Zhang, Y., Kattge, J., Boenisch, G., and others: Global patterns of tree wood density, Global Change Biology, 30, e17224, https://doi.org/10.1111/gcb.17224, 2024.

Yang, Q., Su, Y., Hu, T., Jin, S., Liu, X., Niu, C., Liu, Z., Kelly, M., Wei, J., and Guo, Q.: Allometry-based estimation of forest aboveground biomass combining LiDAR canopy height attributes and optical spectral indexes, Forest Ecosystems, 9, 100059, https://doi.org/10.1016/j.fecs.2022.100059, 2022.

Zanne, A. E., Lopez-Gonzalez, G., Coomes, D. A., Ilic, J., Jansen, S., Lewis, S. L., Miller, R. B., Swenson, N. G., Wiemann, M. C., and Chave, J.: Data from: Towards a worldwide wood economics spectrum (5), https://doi.org/10.5061/DRYAD.234, 2009.

Zobel, B. J. and van Buijtenen, J. P.: Wood Variation and Wood Properties, in: Wood Variation, Springer, Berlin, Heidelberg, 1989.