Beyond species means – the intraspecific contribution to global wood density variation

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Abstract

1 Wood density is central for estimating vegetation carbon storage and a plant functional trait

2 of great ecological and evolutionary importance. However, the global extent of wood density

3 variation is unclear, especially at the intraspecific level.

4

5 We assembled the most comprehensive wood density collection to date (GWDD v.2),

6 including 109,626 records from 16,829 plant species across woody life forms and biomes.

7 Using the GWDD v.2, we explored the sources of variation in wood density within individuals,

8 within species, and across environmental gradients.

9

10 Intraspecific variation accounted for up to 15% of overall wood density variation (sd = 0.068

11 g cm^{-3}). Sapwood densities varied 50% less than heartwood densities, and branchwood

12 densities varied 30% less than trunkwood densities. Individuals in extreme environments (dry,

13 hot, acidic soils) had higher wood density than conspecifics elsewhere (+0.02 g cm^{-3}, ~4% of

14 the mean). Intraspecific environmental effects strongly tracked interspecific patterns (r =

15 0.83) but were only 20–30% as large and varied considerably among taxa.

16

17 Individual plant wood density was difficult to predict (RMSE > 0.08 g cm^{-3}; single-

18 measurement R^2 = 0.59). We recommend (i) systematic within-species sampling for local

19 applications, and (ii) expanded taxonomic coverage combined with integrative models for

20 robust estimates across ecological scales.

21

22 **Keywords:** wood density, functional trait, biomass, intraspecific variation, aridity, hierarchical

23 modelling

24 **1. Introduction**

25 Wood density, the ovendry mass of wood (g) over its fresh volume (cm^{-3}), is an important

26 plant functional trait in ecology and global change studies. Accurate species-level averages of

27 wood density are needed for unbiased estimation of aboveground carbon in vegetation

28 (Phillips et al., 2019). Moreover, wood density defines one of the main axes of global plant

29 trait variation (Díaz et al., 2016). Generally, high-wood density species are less susceptible to

30 mechanical, hydraulic or biotic stress (Chave et al., 2009), experience low mortality at the

31 expense of growth (King et al., 2006; Kraft et al., 2010), and decompose more slowly (Hérault

32 et al., 2010). Wood density therefore displays distinct patterns across successional and

33 environmental gradients (Poorter et al., 2019; Šímová et al., 2018) and is a key factor in the

34 prediction of the global carbon cycle and terrestrial ecosystem dynamics (Sakschewski et al.,

35 2015).

36 Wood density varies widely among woody plants, from species with incredibly low-

37 density wood (~0.10 g cm^{-3} in *Jacaratia spinosa* (Aubl.) A.DC) to species such as lignum vitae

38 (*Guaiacum sanctum* L.) whose wood is denser than water (~1.05 g cm^{-3}) and therefore sinks

39 at any moisture level. However, wood density also varies within and among individuals of the

40 same species (Anderegg et al., 2021; Fajardo et al., 2022; Yang et al., 2023). Intraspecific

41 variation in traits provides an imprint of how organisms react to changes in their environment

42 through adaptation and morphological plasticity (Bolnick et al., 2011; Girard-Tercieux et al.,

43 2023; Moran et al., 2016) and can play an important role in ecosystem functioning (Des

44 Roches et al., 2018). Better knowledge of shifts with ontogeny and along environmental

45 gradients would improve vegetation models (Berzaghi et al., 2020), predict how species

46 ranges shift in response to climatic change and disturbance (Anderegg & HilleRisLambers,

47   2016), and create more robust wood density maps for assessment of functional diversity and

48   vegetation carbon stocks (Boonman et al., 2020; Sæbø et al., 2022).

49   Radial changes within tree trunks and branches are a common source of intraspecific

50   variation in wood density, usually interpreted as a reflection of hydraulic and mechanical

51   changes during ontogeny (Wiemann & Williamson, 1988; Woodcock & Shier, 2002). In plant

52   species with low wood density near the pith, wood density often increases towards the outer

53   trunk layers, while the opposite may occur in plants with high near-pith wood density

54   (González-Melo et al., 2022; Hietz et al., 2013; Longuetaud et al., 2017; Plourde et al., 2015;

55   Woodcock & Shier, 2002), although there are many exceptions to this pattern (Bastin et al.,

56   2015; Osazuwa-Peters et al., 2014). A link between radial variation in wood density and plant

57   ecological strategies has also been suggested: pioneer plants have low density wood and grow

58   fast early on, but invest in denser tissues as individuals mature. In contrast, shade-tolerants

59   build dense tissues initially, but may invest more in diameter growth than tissue density when

60   reaching the canopy (Bastin et al., 2015; Woodcock & Shier, 2002). However, we do not know

61   how consistent and important these patterns are at global scales. Radial changes in wood

62   density do not always map onto ecological strategies (Hietz et al., 2013), may be influenced

63   by deposition of chemical compounds in heartwood (e.g., non-structural, secondary

64   metabolites known as "extractives", Lehnebach et al., 2019), and vary among conspecific

65   individuals or even within individuals (Osazuwa-Peters et al., 2014).

66   Wood density also varies along the hydraulic pathway and across plant organs within

67   an individual, another source of intraspecific variation (Longuetaud et al., 2017; Momo et al.,

68   2020; Schuldt et al., 2013). In trees, for example, wood density has been hypothesized to

69   increase from trunks to branches, because high density should provide more benefits to

70   mechanical stability in horizontal branch than vertical trunk wood (Anten & Schieving, 2010;

71 van Casteren et al., 2012). However, while branch and trunk wood densities are generally

72 tightly correlated with one another, there is little agreement on whether branches are more

73 (Billard et al., 2020; Dibdiakova & Vadla, 2012; Fajardo, 2018; Fegel, 1941) or less dense than

74 trunks (He & Deane, 2016; Sarmiento et al., 2011; Swenson & Enquist, 2008), and there is also

75 variation within trunks and branches (Schuldt et al., 2013; Terrasse et al., 2021). A

76 confounding factor may be that wood density varies less in branches than in trunks: data from

77 temperate ecosystems show that wood density increases from trunk to branches in species

78 with low-density trunk wood and shows the opposite pattern in species with high-density

79 trunk wood (MacFarlane, 2020). It is unclear whether this pattern generalizes across biomes

80 and also whether it reflects different functional requirements of branches and trunks.

81 However, it has been hypothesized that trunk-branch gradients simply reflect radial

82 ontogenetic patterns between juvenile and mature wood, since more distal organs are

83 younger and contain higher fractions of sapwood (Gartner, 1995).

84   Wood density also varies across individuals of the same species due to differences in

85 genetics and environments (Zobel & van Buijtenen, 1989). As environmental conditions

86 become more extreme (drier, less fertile, more shaded, more windy), species are expected to

87 grow more slowly and invest more resources in dense and stress-resistant tissues (Chave et

88 al., 2009). Similar effects are expected within species (Anderegg et al., 2021). For example,

89 individuals that build tissues with narrow conduits and thick fibre and conduit walls should be

90 more resistant to embolism (Hacke et al., 2001; Olson et al., 2020). In contrast, in warm, fertile

91 and frequently disturbed environments with high plant turn§over, fast-growing individuals

92 with low wood density are expected to be more competitive and successful (Muller-Landau,

93 2004; Yang et al., 2023). However, genetic control over wood density is high, suggesting that

94 the variation among individuals of the same species is limited (Zobel & Jett, 1995). Wood

95   density variation may also be limited by covariation with other traits, and trade-offs between

96   different wood functions (Anderegg & HilleRisLambers, 2016; Ziemińska et al., 2013). For

97   example, low-density wood can sometimes be beneficial even in harsh conditions, as low-

98   density species tend to have greater water storage and capacitance (Ziemińska et al., 2020),

99   a potential advantage in dry environments.

100   Overall, theory, empirical observations, and common sense predict that wood density

101   varies predictably within species. However, while many studies find that intraspecific

102   variation is predictable (Anderegg et al., 2021; Anderegg & HilleRisLambers, 2016; Farias et

103   al., 2023), just as many do not (Fajardo, 2018; Richardson et al., 2013; Rosas et al., 2019;

104   Umaña & Swenson, 2019). Intraspecific variation is generally smaller than interspecific

105   variation (Osazuwa-Peters et al., 2014), so it is easily confounded with measurement errors

106   and methodological differences in how wood density is determined (Barbosa & Fearnside,

107   2004; Jati et al., 2014; Vieilledent et al., 2018; Williamson & Wiemann, 2010). To date, the

108   largest global wood density collections, including the GWDD v.1 (Zanne et al., 2009), do not

109   systematically record the tissue types and plant organs where measurements were taken. As

110   a result, there is a fundamental lack of knowledge about the extent of intraspecific variation

111   in wood density, its determinants within and among individuals, and its implications for

112   ecological models and carbon estimates in woody ecosystems. In particular, we lack practical

113   guidelines as to when to exhaustively measure it versus when it can be safely ignored.

114   Here, we introduce a substantially updated and improved version of the Global Wood

115   Density Database (GWDD v.2), which more than doubles the taxonomic coverage of the

116   original database (from 7,555 to 16,829 taxonomically resolved species), increases the

117   number of records from 16,468 to 109,626, and, as available, includes a detailed description

118   of where and how measurements were taken within and across individuals. Using these data,

119   we addressed the following questions: 1. How large is intraspecific variation in wood density?

120   2. How much of this intraspecific variation can be explained by differences in wood density

121   among plant organs? 3. How much of intraspecific variation can be explained by

122   environmental factors, such as temperature, water deficit, wind speeds and soil fertility?

123   Based on our results, we also 4. make a number of recommendations to effectively

124   incorporate variation among and within individual plants into models to improve predictions

125   of wood density.

2. Methods

2.1 Assembling the Global Wood Density Database v.2

The GWDD v.2 is a substantial update of the GWDD v.1, an open-access database that consisted of a list of 16,468 tissue density values from ca. 7,500 species. It was assembled from more than 200 sources and included a taxonomic identifier, a region where the measurement was taken, and a literature reference (Chave et al., 2009; Zanne et al., 2009). Since its publication, many new wood density values and large trait databases have been published, and improved methodologies have been developed to improve consistency across studies (Cuny et al., 2025; Farias et al., 2020; Langbour et al., 2019; Radtke et al., 2023; Vieilledent et al., 2018; Williamson & Wiemann, 2010). We used this as an opportunity to expand the database and create a new, improved version.

First, we critically re-examined the original database and updated 42% of entries (n = 6,968, details in Supplementary S1). Second, we included additional wood density measurements from published and unpublished sources (cf. Supplementary S1). We put particular emphasis on previously undersampled biomes, such as dry forests, savannas, and the species-rich tropics. We also included individual measurements instead of aggregated values and created a comprehensive documentation. The new database contains 45 attributes that report the original values, sampling techniques, and data transformation methods (Table S1). The database is available online on Zenodo (doi: 10.5281/zenodo.16919509, embargoed until acceptance for publication).

Wood density definition and conversion factors

In the GWDD v.2 and throughout this study, wood density is defined as 'basic' wood density, the mass of an oven dried wood sample divided by its fresh volume (g cm^{-3}). Wood density

150   thus measures the dry mass contained in the wood volume of live plants and is an indicator

151   of a plant's investment in woody tissues. When normalized by the density of water (1 g cm^{-3}),

152   it is also referred to as "wood specific gravity" (g g-1; Williamson & Wiemann, 2010), but

153   throughout our analyses, we use the term "wood density". When assembling the GWDD v.2

154   and in all following analyses, we also included the tissue densities of tree-like monocots

155   without secondary growth, as this was consistent with common inventory protocols (Condit,

156   1998; The SEOSAW Partnership, 2021) and global tree databases (e.g., Beech et al., 2017). In

157   total, monocots contributed 186 records from 91 species most of which were either

158   Arecaceae (65) or Asparagaceae (18). Since these monocots amounted to less than 0.2% of

159   the total records, their inclusion had a negligible effect on results.

160   Different wood density definitions are available in the literature. Green density, the

161   fresh mass of wood divided by fresh volume, reflects actual plant growing conditions (Niklas

162   & Spatz, 2010). In the timber industry, a relevant quantity is airdry wood density, the mass of

163   wood divided by its volume, with both measured at ambient air moisture (~10-15%),

164   reflecting properties of wood in the conditions in which it is used (Détienne & Chanson, 1996;

165   FPL, 1999). Ovendry density, i.e., dry mass over dry volume, has also been reported in the

166   literature (Deklerck et al., 2019), and dendrochronological studies often derive correlates of

167   wood density variation within and between tree rings with X-ray techniques (Jacquin et al.,

168   2017). Fortunately, air- and ovendry densities can each be converted into basic density

169   through physical conversion factors (Brown, 1997; Ilic et al., 2000; Sallenave, 1971), and

170   recent research has shown that this can be done with as little error as 0.015 g cm^{-3} (ca. 2.5%

171   of typical mean wood density, Vieilledent et al., 2018). These factors were also applied in the

172   construction of the GWDD v.2 to maximize the taxonomic and geographic coverage of wood

173   density. Converted values and the source quantity were recorded in the columns

174 *value_reference* and *quantity_reference*, the conversion factor in *wsg_conversion*, and the

175 derived basic wood density value as *wsg* ("wood specific gravity").

176

177 *Aggregation levels*

178 The GWDD v.2 provides extensive information on where and how records were obtained,

179 which was not available in the GWDD v.1. These new variables include *site*, an informal

180 description of the measurement site, *longitude* and *latitude* in the decimal system, and

181 *country*. The attribution to a *region* has been revised since GWDD v.1 to better reflect

182 geographical variation (Table S1). The database also contains information on sample type

183 (*type_sample* for "core" or "disk"), measurement location within plants (*location_sample* for

184 "trunk", "branch" or "root", for example, and *type_tissue* for "heartwood", "sapwood" or

185 "bark"), whether a particular wood density value is the mean value of multiple individual

186 plants (*plant_agg*), and how many individuals were aggregated (*plants_sampled*). If several

187 measurements were available for the same individual, they were recorded with the same

188 *id_plant*. Direct estimates of variation around mean values were not included in the GWDD

189 v.2, as they were not consistently reported in the literature. Where detailed measurement

190 information was not available, attributes were left empty ("NA"). These samples were

191 excluded from analyses of intraspecific wood density variation in this study.

192

193 *Taxonomic name resolution*

194 Taxonomic names were newly standardized via the *WorldFlora* R package (Kindt, 2020) and

195 the June 2023 version of the *World Flora Online* (WFO) database (The World Flora Online

196 Consortium   et   al.,   2023).   Taxon   names   were   converted   in   the   field

197 *species_reference_canonical*, including infraspecific assignations (e.g., variety, subspecies,

198   hybridization) and resolved via the default fuzzy matching in the *WorldFlora* package.

199   Taxonomic authorities were not included as inputs for the matching, as they were

200   inconsistently reported in the source data. For unmatched taxa and anything beyond a

201   missing, added or switched letter, the matching was repeated without infraspecific

202   assignations. In the case of multiple matches, we chose the default value provided by *World*

203   *Flora Online* (called "smallest id"). Any remaining taxa were manually corrected. We also

204   extracted information on plant families from the WFO database and reported it in the GWDD

205   v.2. Overall, only 34 entries (22 genera) could not be matched to any family.

206   Taxonomies are constantly updated to resolve ambiguities in species definitions, and

207   sometimes, taxonomic resolution leads to a reclassification of species as subspecies and

208   varieties (or vice versa). For simplicity, we recorded the entire scientific name provided by

209   *WorldFlora* in the GWDD v.2's *species* column, including infraspecific epithets. We also used

210   this species definition for analyses in our study to provide the most conservative estimates of

211   intraspecific variation. However, preliminary tests revealed that only a negligible portion of

212   the analysed species had infraspecific epithets (~1% of all species with individual level wood

213   density records, <1% among high-quality records), so this choice had no discernable effect on

214   results.

215

216   **2.2. Intraspecific wood density variation**

217   *Coverage of taxonomic and geographic variation*

218   Overall, we assembled more than 100,000 records from ca. 17,000 plant species in the GWDD

219   v.2. We assessed the representativeness of the species included in the GWDD v.2 with regard

220   to the number of woody taxa worldwide estimated by assuming that 45% of the flowering

221   plants are woody (FitzJohn et al., 2014), and the total number of flowering plants is ca.

222   400,000 (Enquist et al., 2019). We also used a verified list of known tree species

223   (GlobalTreeSearch 1.7; Beech et al., 2017), resolved via *World Flora Online* for consistency, to

224   assess which percentage of tree species in each country had a corresponding wood density

225   estimate in the GWDD v.2. Intraspecific coverage was assessed through the number of

226   records per species.

227

228   *Statistical analysis of intraspecific wood density variation*

229   To assess the extent and drivers of intraspecific wood density variation, we examined

230   measurements from multiple sites per species, multiple individuals per site and multiple

231   measurement locations per individual. For some species, the database contains multiple

232   samples of individuals, but only from a single site, while for others, the database contains

233   samples from multiple sites, but each with a single individual. To address this issue, we

234   created subsets of the GWDD v.2 for each question, and alternative modeling strategies to

235   ensure robustness of results (see Table S3 for an overview of models and subset sizes).

236   Throughout, 'intraspecific variation' refers to cases where biological variation can be

237   confidently separated from measurement errors. For example, tissue type

238   (heartwood/sapwood) and environmental factors should affect biological variation, not

239   measurement error. By contrast, when variation cannot be attributed to a specific factor,

240   intraspecific variation plus measurement error are referred to as the '(residual) wood density

241   distribution'.

242   Across all datasets, we removed records not identified to species level ("genus" in the

243   *rank_taxonomic* column of the database), samples consisting of bark ("bark" in the

244   *type_tissue* column of the database), and records from experiments (identified by the words

245   "fertilizer" or "treatment" in *experiment_design*) or from plantations (recorded as

246 "plantation" in *type_forest)*. We also excluded root samples ("root" in the *location_sample*

247 column) due to small sample sizes.

248   Unless otherwise stated, all datasets were analyzed using mixed effects models with

249 varying random slopes and intercept terms and qualitative explicative variables (e.g.,

250 "sapwood" vs. "heartwood") coded as numerical variables (0, 1). Models were fitted in the R

251 environment (R Core Team, 2023), both with a Bayesian approach – using the *brms* package

252 (Bürkner, 2018) and the STAN software (Carpenter et al., 2017) – and the maximum likelihood

253 framework using the *lme4* package (Bates et al., 2015, 'bobyqa' optimizer). The Bayesian

254 approach is the default, due to flexibility in model construction, regularization through priors

255 and full propagation of uncertainty. All models were assessed for convergence using standard

256 diagnostics (R-hat <= 1.02) and posterior predictive checks (further details in S3, Table S3 and

257 Fig. S1). Throughout, we also report *lme4* estimates, as they are less expensive

258 computationally and thus more readily used in practice, especially when relying on large

259 databases.

260

261 *Quantification of intraspecific variation in wood density*

262 To assess the overall extent of intraspecific variation in wood density, we first partitioned

263 total wood density variance and its components. We fitted a model with random effects for

264 species nested within genera, genera nested within families, and a crossed random effect for

265 methodological bias (the bibliographic reference or "source", model M1, Table S3). We

266 computed variance as the sum of variances across levels plus residual variance. To assess

267 robustness, we also fitted a separate model without the "source" effect (Table S3, M2) and

268 restricted the analysis to species with ≥ 3 individuals per species, ≥ 3 species per genus, ≥ 3

269 genera per family (n = 49,991, $n_{species}$ = 2,735; Tables M3-4).

270   Second, to assess the contribution of different sources of intraspecific variation to its

271   overall extent, we partitioned the intraspecific variance of wood density. We did so by fitting

272   models with random effects for individuals nested within sites, and sites nested within

273   species, each time with and without a crossed effect for measurement source (formulas in

274   Table S3, M5-8). We restricted the analysis to subsets of species present in at least k sites,

275   one site with at least k individuals, and one individual with at least k measurements (first

276   setting k = 2 and then repeating for k = 3). Sites were defined as the collection of data within

277   the same 1 km^2 grid pixel. This approach mirrored the resolution of the climate input data

278   and accounted for geolocation uncertainty (e.g., rounding of longitude and latitude values to

279   2 decimals). Data subsets comprised n = 19,246 ($n_{individual}$ = 14,373, n_{site} = 1,270, $n_{species}$ = 147)

280   records for k=2, and n = 2,494 ($n_{individual}$ = 1,052, n_{site} = 233, $n_{species}$ = 35) for k=3.

281   The shape of intraspecific wood density distributions was assessed through the direct

282   modeling of the residual variance parameter σ (Table S3, model M1, cf. Supplementary S3)

283   and by comparing how well normal and lognormal distributions fitted each species' wood

284   density distribution (Shapiro-Wilkes test for untransformed vs. log-transformed wood

285   densities with $p < 0.05$). To account for methodological differences and report biological

286   variation, we always subtracted the random "source" effect before reporting wood density

287   variation.

288

289   *Estimating variation in wood density within individuals*

290   Variation in wood density within individuals was assessed by subsetting to species with

291   measurements for both sapwood and heartwood (n = 679, $n_{species}$ = 150), or for both

292   trunkwood and branchwood (n = 48,494, $n_{species}$ = 2,018). The fitted models (Table S3, M9-10)

293   had fixed effects for either sapwood (0 for heartwood, 1 for sapwood) or branchwood (also

294   0/1), random intercepts and slopes at species level, and a crossed random effect for

295   measurement source. To assess whether wood density followed predictable gradients from

296   the pith outwards to the bark and from the trunk upward to the branches, we calculated

297   species means for each woody component and checked whether the slopes of major axis

298   regressions (lmodel2 package; Legendre, 2018) of sapwood vs. heartwood and branchwood

299   vs. trunkwood densities were < 1 (indicating a decrease) or > 1 (indicating an increase, Table

300   S3, M11-12).

301   To assess robustness and potential confounding effects, such as higher sapwood

302   fraction in branches or variation in sample sizes among taxa, we repeated the analysis with a

303   subset of branchwood and trunkwood densities taken entirely from sapwood (n = 1,193,

304    $n_{species}$ = 523, M13), with a higher-quality dataset (species with >= 5 measurements both for

305   branches and trunks, selecting 5 random measurements from each, $n_{species}$ = 189, M14), and

306   a subset of records where both branch and trunk samples were taken from the same

307   individuals (n = 3,527, $n_{species}$ = 145, M15, fitted at individual plant level, taking a random

308   sample from both trunk and branch).

309

310   *Environmental predictors of intraspecific wood density variation*

311   To examine wood density variation across environmental gradients, we used species sampled

312   from at least two sites, and paired them with the following bioclimatic layers that represent

313   multiple axes of plant environmental gradients including extremes: annual mean temperature

314   (°C), site water balance (kg m^{-2} yr^{-1}, but with the sign reversed to indicate water deficit) and

315   mean wind speed (m s^{-1}) at 1 km resolution. We used the data from the CHELSA/BIOCLIM+

316   climatology 1981-2010 (Brun et al., 2022; Karger et al., 2017), but also repeated the analysis

317   with products from the TerraClimate climatology 1981-2010, relying on climatic water deficit

318   (mm) instead of site water balance (Abatzoglou et al., 2018). While site water balance is a

319   general measure of the availability of water to plants (Brun et al., 2022), climatic water deficit

320   directly measures drought stress as the difference between potential and actual

321   evapotranspiration. We also included the following soil layers: sand fraction (g kg^{-1}), pH

322   (unitless) and cation exchange capacity (in mmol(c) kg^{-1}), based on the *soilgrids* product

323   (Hengl et al., 2017). By default, we report only effects that remained qualitatively consistent

324   across analyses methods (no shift in sign). For simplicity, effect sizes are always taken from

325   the full dataset using CHELSA/BIOCLIM+ predictors.

326   We matched predictors to wood density observations and assessed environmental

327   effects both among and within species with the following model (cf. Table S3, M16-19):

328    $wd_{ij} = \beta_0 + \sum_{k=1}^{n} \beta_k \cdot env_{kj} + \sum_{k=1}^{n} \gamma_k \cdot \Delta env_{kij} + \gamma_{0j} + \sum_{k=1}^{n} \gamma_{kj} \cdot \Delta env_{kij} + \varepsilon_{ij},$

329   with $\varepsilon_{ij} \sim N(0, \sigma^2)$. Here, *n* is the number of individuals, wd_{ij} is the wood density of

330   individual *i* belonging to species *j*, env_{kj} the environmental variable *k* averaged across all

331   individuals from species *j* and Δenv_{kij} the same environmental predictor *k*, but group-centred

332   around the species mean value, and ε_{ij} is the error. The model thus partitions environmental

333   effects into interspecific effects, where env_{kj} is the typical environment of species *j*, and

334   intraspecific effects, where Δenv_{kij} represents how much the individual *i* deviates from the

335   species mean environment. The model is equivalent to a standard linear-mixed effects model

336   with random slopes and intercepts for species, but with added group-level predictors env_{kj}

337   that control for predictable variation among species (Table S3, models M16-17, Bafumi &

338   Gelman, 2011). β_0 is the overall intercept, β_k and γ_k are fixed-effect parameters, and γ_{0j} and

339   γ_{kj} are random intercept and slope parameters for species *j*, respectively. We chose this

340   model as it allows for partitioning of intra- and interspecific effects and is more robust when

341   predictors vary systematically with grouping factors (Bafumi & Gelman, 2011).

342   Since some species may cover only a narrow environmental range, we repeated the

343   analysis with a subset of species for which at least one environmental factor covered a large

344   range (Table S3, n = 30,128, $n_{species}$ = 692, M18-19), defined via TerraClimate and 5 km *soilgrids*

345   as the 90th percentiles of all species' ranges ($\Delta_{Temperature}$ >= 8°C, $\Delta_{Water\ Deficit}$ >= 450 mm, Δ_{Wind}

346      $_{speed}$ >= 1.8 m s^{-1}, $\Delta_{Sand\ content}$ >= 300 g kg^{-1}, Δ_{pH} >= 1.5 or $\Delta_{Cat.\ exch.\ cap.}$ >= 165 mmol(c) kg^{-1}). To

347   assess the consistency of predictors across biomes, we fitted separate models for tropical

348   species (≥ 3 measurements in the tropics, n = 8,783, $n_{species}$ = 700, M20-21) and extratropical

349   species (≥ 3 measurements outside the tropics, n = 26,437, $n_{species}$ = 247, M22-23).

350   In all models, intra- and interspecific effects were examined on the same standardized

351   scale. However, as environmental gradients among species were larger than among

352   individuals of the same species, we also tested the rescaling of effect sizes to realized

353   environmental ranges for the tropical and extratropical subsets, i.e. standardizing *after*

354   separation of intra- and interspecific effects by their respective standard deviations. We fitted

355   additional models to gymnosperms only (Table S3, n = 12,089, $n_{species}$ = 59, M24-25) to assess

356   the stability of global effects when sampling is reduced to a small number of anatomically

357   diverging taxa.

358

359   *The effect of intraspecific variation on wood density predictions*

360   Since wood density measurements are destructive, samples are usually only taken from a

361   subset of plants, from nearby conspecifics or from global databases. The samples are then

362   used to predict the wood density of the remaining individuals, for example, by using species

363   mean values, or, if those are not available, the average of wood densities from the same genus

364   or plot (Flores & Coomes, 2011; Réjou-Méchain et al., 2017). If many traits have been

365   measured, more complex imputation methods are available (Schrodt et al., 2015). However,

366 most methods risk confounding intraspecific and interspecific variation and it is unclear what

367 to do in edge cases, e.g., if 1-2 measurements from the same species are available, is it better

368 to estimate an individual's wood density by (i) directly using these values and averaging them,

369 (ii) attributing the genus mean value, or (iii) combining both types of information, e.g.,

370 through taxonomic or phylogenetic hierarchical modelling? It is also (iv) unclear if local

371 measurements should be weighted more strongly to account for environmental gradients in

372 wood density.

373   To answer these questions, we first assessed the influence of intraspecific variation

374 on species-level wood density estimates. We computed average wood densities for all species

375 with more than five measurements ($n_{species}$=1,667) and assessed how accurately these

376 reference values could be predicted if species were not well sampled. To do so, we cycled

377 through all 1,667 species, in turn removed either all species-specific measurements or all

378 species-specific measurements except one or two randomly chosen ones, and then estimated

379 the species' mean wood density from the remaining data. The estimation was carried out with

380 three models: i) the default approach of estimating wood density means from a genus average

381 (when no species-specific measurements exist) or a species average (when one or two

382 species-specific measurements exist), ii) a hierarchical model of wood density that included a

383 nested taxonomic structure (*family / genus / species*) and nested random effects for sites

384 within studies, and iii) the same model as in ii), but with an optional fixed effect for trunkwood

385 vs. branchwood (Table S3, models M26-27). Model performance was estimated via root mean

386 square error (RMSE, g cm^{-3}) and R^2 (Table S16).

387   Second, we tested how accurately we could predict the wood density of an individual

388 plant depending on how well the species was sampled locally. To do so, we selected species

389 with measurements from at least 3 sites, and where at least 4 of its individuals were measured

390   at each of the 3 sites ($n_{species}$ = 318). For each of the individuals, we then reduced the set of

391   locally measured conspecifics to 0, 1, 2, or 3 (selecting random individuals where possible),

392   and for each case tested how well the individual's wood density could be inferred from the

393   remaining data. We tested five models: i) a species average across the entire dataset, ii) a

394   species average, but using only values measured as part of the same study, iii) a species

395   average, but using only values measured locally, and iv) and v) the same hierarchical models

396   as described above (Table S3, M26-27). Model performance was estimated via root mean

397   square error (RMSE, g cm^{-3}) and R^2 (Table S17).

398   **3. Results**

399   *The Global Wood Density Database*

400   To create the GWDD v.2, we assembled 109,626 wood density records from 166 countries,

401   617 primary sources and 17,262 taxa across all woody biomes and biogeographic realms. Of

402   these taxa, we resolved 16,829 to species level. We also included information on aggregation

403   levels, conversion factors and precise geographic location, as well as an additional 15,093 bark

404   density records from 57 studies. The fully assembled GWDD v.2 contained 6.7x as many wood

405   density records and 2.3x as many species as the GWDD v.1 (16,468 records across 7,453

406   accepted species). We estimated that the GWDD v.2 covered 10% of all woody species, 24%

407   of all known tree species and 49% of gymnosperm species. Of the families with the most

408   known tree species, Sapotaceae and Fabaceae were best represented in the database (38%

409   and 34% coverage). In contrast, wood density estimates were rare in Arecaceae (6%, not true

410   wood), Araliaceae (10%) and Melastomataceae (12%).

411   Out of all the GWDD v.2's records, 83,502 (76%) were provided at individual plant

412   level, and 58,675 entries (54%) were precisely geolocated. For 4,508 species, at least five

413   wood density measurements were available, and combinations of branch-trunk wood

414   measurements were available for 2,018 species (146 families). For 78 species, mostly in

415   Pinaceae and Fagaceae, there were more than 100 wood density measurements. The majority

416   (65%) of the wood density values were directly measured as basic wood density (71,746). The

417   remaining values were converted from airdry (~29%), and ovendry wood densities (~6%).

418   Geographic coverage varied widely, from a near-complete coverage of recorded tree species

419   in high latitudes to < 50% in tropical regions (95% range: 27.3%; 98.5%, Fig. 1). An exception

420   was West Africa where coverage of known tree species was ≥70%, albeit without precise

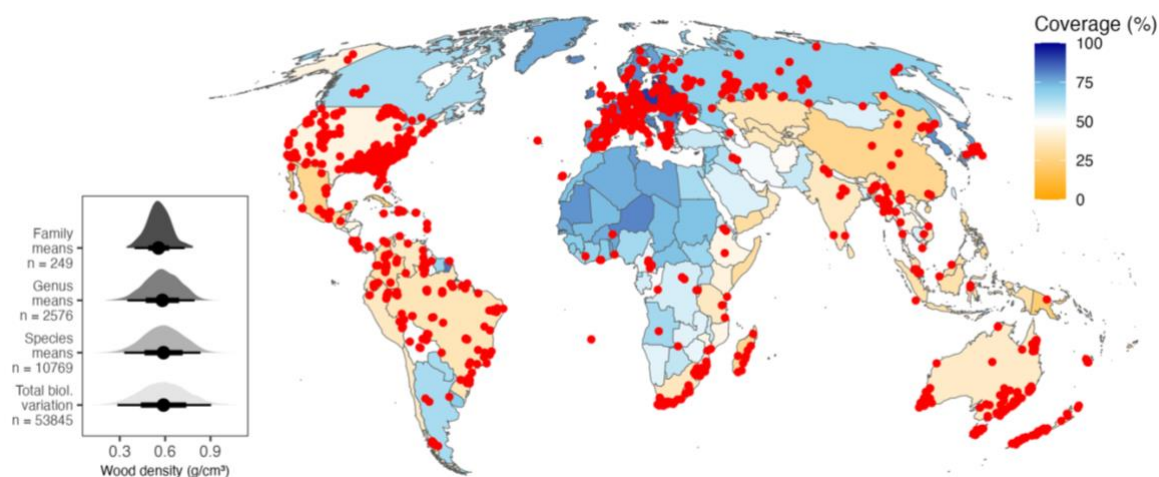421   geolocation for most records (cf. limited number of red dots in Fig. 1).

Fig. 1: Geographic coverage of the Global Wood Density Database (GWDD) v.2. This figure separately maps 1) the percentage of each country's species that could be matched to species in the GWDD v.2 (background colour gradient), and 2) all locations with explicitly geolocated wood density measurements in the GWDD v.2 (red dots). For the former, measurements did not have to be explicitly geolocated, meaning some countries had high species coverage, despite a lack of country-specific wood density measurements (e.g., West African countries). Conversely, some large, predominantly temperate countries (e.g., the U.S.) had many explicitly geolocated records, but also covered species-rich subtropical and tropical zones, which lowered their overall species coverage. Country boundaries follow *Natural Earth* (https://www.naturalearthdata.com/, last accessed 14 Dec 2023). The inset in the lower left corner shows the distributions of wood density at various levels of aggregation: distributions of family, genus and species means, as well as the full biological variation in wood density. To attenuate sampling biases, the distributions were based on five random draws from each species (with replacement). Biological variation was estimated by subtracting inferred methodological biases ("source" effect in model M1, Table S3) from the raw values.

The extent and shape of intraspecific variation in wood density

Globally, wood density displayed a normal distribution with a mean of 0.56 g cm^{-3} (sd = 0.178 g cm^{-3}, Fig. 1 inset). The majority of this variation (77%, sd = 0.156 g cm^{-3}) was accounted for by variation at the taxonomic family (30%), genus (30%) or species levels (17%), with the rest attributed to study methodology (8%) or intraspecific variation and unknown errors (15%; 0.068 g cm^{-3}, Fig. 1, inset, Fig. S2-3, Table S4). The intraspecific contribution was robust to model details (Table S4, Table S5). For well-sampled taxa, we further partitioned intraspecific variance, and found that wood density variation among sites exceeded variation among

445 individuals within sites (sd = 0.025-0.042 g cm^{-3} vs. sd = 0.017-0.028 g cm^{-3}, Table S6), but was

446 small overall (ca. 20-30% of total intraspecific variation), and smaller than residual variation

447 (variation within individuals + unknown measurement error, sd = 0.040-0.045 g cm^{-3}, Table

448 S5-6).

449 Intraspecific variation differed in extent and shape between species, with a few

450 species varying much more than the others (Fig. S3, e.g., sd = 0.094 g cm^{-3} for *Quercus ilex*,

451 compared to sd = 0.038 g cm^{-3} for *Quercus alba*). The distribution of wood density values of

452 conspecifics was generally heavy-tailed, but there was no clear signal of skew, with the

453 lognormal distribution more often rejected than the normal distribution (13.7% vs. 12.6%,

454 Shapiro-Wilkes $p < 0.05$ for log-transformed and untransformed values).

455
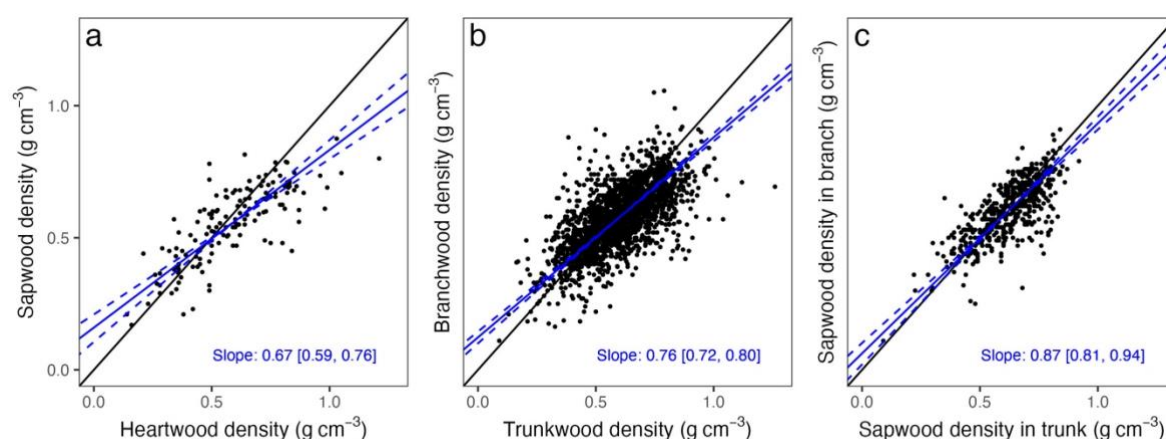
456 **Fig. 2: Variation in wood density across plant tissue types.** Shown are plots of species means for a) heartwood

457 vs. sapwood densities, b) trunkwood vs. branchwood densities and c) trunkwood vs. branchwood densities when

458 measured on sapwood. Every dot represents a species, blue lines are Major Axis regression lines, *dashed* lines

459 their 95% CI. Solid black lines are the 1:1 lines.

460

461 *Wood density variation within individuals*

462 Across plant tissue types, there were strong correlations between heartwood and sapwood

463 densities (Pearson's r = 0.78, Fig. 2a) and between trunkwood and branchwood densities (r =

464   0.67, Fig. 2b, Table S9). However, slopes were < 1 in both cases. There was a 50% reduction

465   in the variance of sapwood compared to heartwood (0.144 vs. 0.197 g cm^{-3}) and a ~30%

466   reduction in the variance of branchwood compared to trunkwood (0.120 g cm^{-3} vs. 0.145 g

467   cm^{-3}). When comparing only sapwood samples from trunks and branches, this effect was

468   weaker (0.112 vs. 0.124 g cm^{-3}, less than a 20% reduction in variance) and the correlation was

469   stronger (r = 0.76, n = 523, Fig. 2c; for more analyses see Table S9, Figs. S5-S6). There was a

470   weak average decrease from heartwood to sapwood of -0.001 g cm^{-3} and a stronger, but still

471   small decrease of -0.023 g cm^{-3} from trunkwood to branchwood (Table S8). However, both

472   effects varied strongly among species (slope sd = 0.060 g cm^{-3} for heartwood vs. sapwood and

473   sd = 0.075 g cm^{-3} for trunkwood vs. sapwood).

474

475   *Wood density variation among individuals*

476   Among individuals within species, environmental factors had small, but consistent, effects on

477   wood density variation (Fig. 3, Tables S10-13, Fig. S7-10). Wood density increased with

478   temperature by 0.012 g cm^{-3} (standardized effect size) and with water deficit by 0.010 g cm^{-}

479   ^{3}; it decreased weakly with wind speed and soil pH (by -0.003 for both, Tables S10-11). These

480   effects were strongly correlated with interspecific effects (r = 0.83, Fig. S12), but were smaller

481   by 70-80% (Fig. 3, Figs. S7-10, Tables S10-13) and varied from one species to another. For

482   example, a typical intraspecific increase in wood density by 0.010 g cm^{-3} amounted to ~25%

483   of the respective interspecific effect (0.038 g cm^{-3}), and species varied widely around this

484   mean (sd = 0.038 g cm^{-3}, Table S10). Patterns were comparable when modelling tropical and

485   extratropical species separately, but in the tropics, increases with water deficit (0.012 g cm^{-3}

486   within and 0.059 g cm^{-3} among species) and decreases with pH (-0.014 within and -0.033 g

487   cm^{-3} among species) were stronger. In a separate analysis for gymnosperms, there was a clear

488   intraspecific decrease of -0.010 g cm^{-3} with soil pH and a strong intraspecific increase with

489   water deficit (0.034 g cm^{-3}, Table S15, Fig. S11). Since some species covered a narrow

490   environmental gradient, effects were weaker when rescaling effect sizes to realized

491   environmental ranges (Table S14, Figs. S13-14). For example, within the actual environmental

492   limits of species observed in our data, tropical wood density increased by 0.012 g cm^{-3} with

493   temperature instead of the 0.022 g cm^{-3} predicted by a more generic model.

494
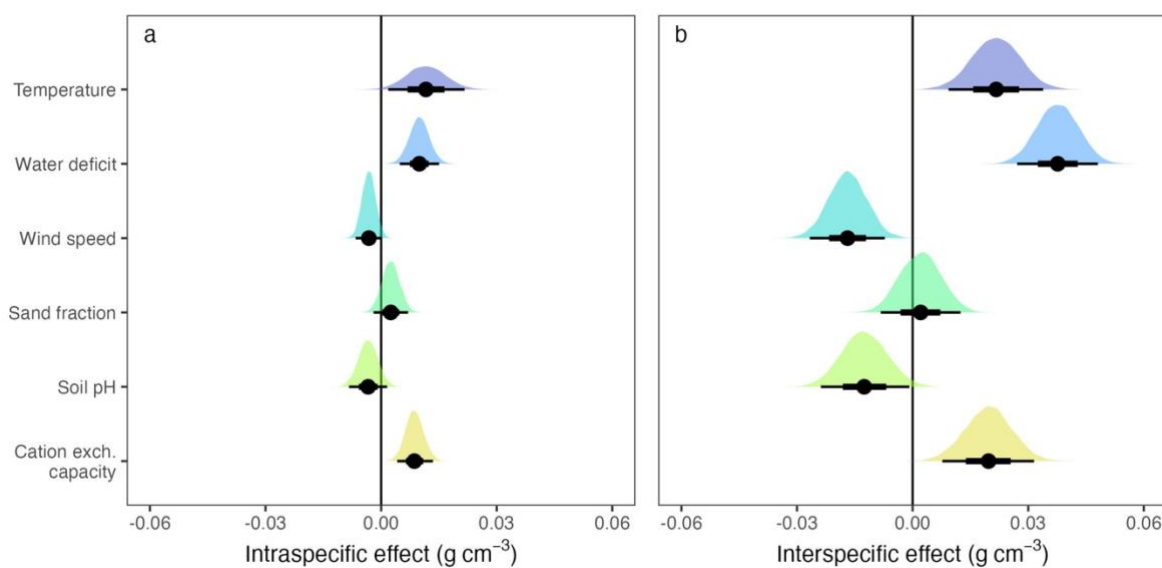
495   **Fig. 3: Environmental effects on wood density.** Shown are the global effects of climatic and edaphic predictors

496   on wood density, separated into intraspecific (a) and interspecific effects (b). Estimates of effect sizes were

497   derived from a Bayesian hierarchical model, with all predictors scaled by one standard deviation (model M9, cf.

498   Table S3 and Table S10). Climatic variables were from CHELSA/BIOCIM+ (Brun et al., 2022; Karger et al., 2017),

499   edaphic variables from *soilgrids* (Hengl et al., 2017). Black dots indicate the median effect size and black intervals

500   indicate quantile ranges (66% and 95%, partially covered by the black dots). The effects of cation exchange

501   capacity were highly dependent on grid cell resolution and models, meaning effect sizes should be interpreted

502   with caution (Fig. S7).

503

504   *The effect of intraspecific variation on wood density estimation*

505   Intraspecific variation strongly reduced the accuracy of wood density estimates in

506   undersampled species. A single wood density measurement was a poor approximation of the

507   species mean (RMSE = 0.084 g cm^{-3}); it was in fact comparable to a genus mean that did not

508   involve any sampling of the target species (RMSE = 0.083 g cm^{-3}, Table S16). However, the

509   accuracy of species-level wood density estimates improved quickly with better sampling.

510   From the average of two measurements, species-level wood density could already be

511   predicted with RMSE = 0.056 g cm^{-3} (Table S16). Accuracy improved further when applying

512   hierarchical models that combined individual measurements with taxonomic information

513   from the remainder of the GWDD v.2 (RMSE = 0.038 g cm^{-3} for two measurements, Tables

514   S16-17).

515   The wood density of individual plants was much harder to predict from conspecifics,

516   with an RMSE of 0.107 g cm^{-3} and R^2 = 0.59 when estimated from a single local wood density

517   measurement (Fig. 4a, Tables S16-17). Errors were lower when pooling information with the

518   GWDD v.2 via hierarchical modelling, but the improvements were moderate (RMSE = 0.086 g

519   cm^{-3} or ca. 20% of the raw estimate, and R^2 = 0.71, Fig. 4b). Errors were similar when three

520   measures from local conspecifics were included, both as simple average (RMSE = 0.082 g cm^{-}

521   ^{3}) or based on a hierarchical model (RMSE = 0.083 g cm^{-3}, Table S17).
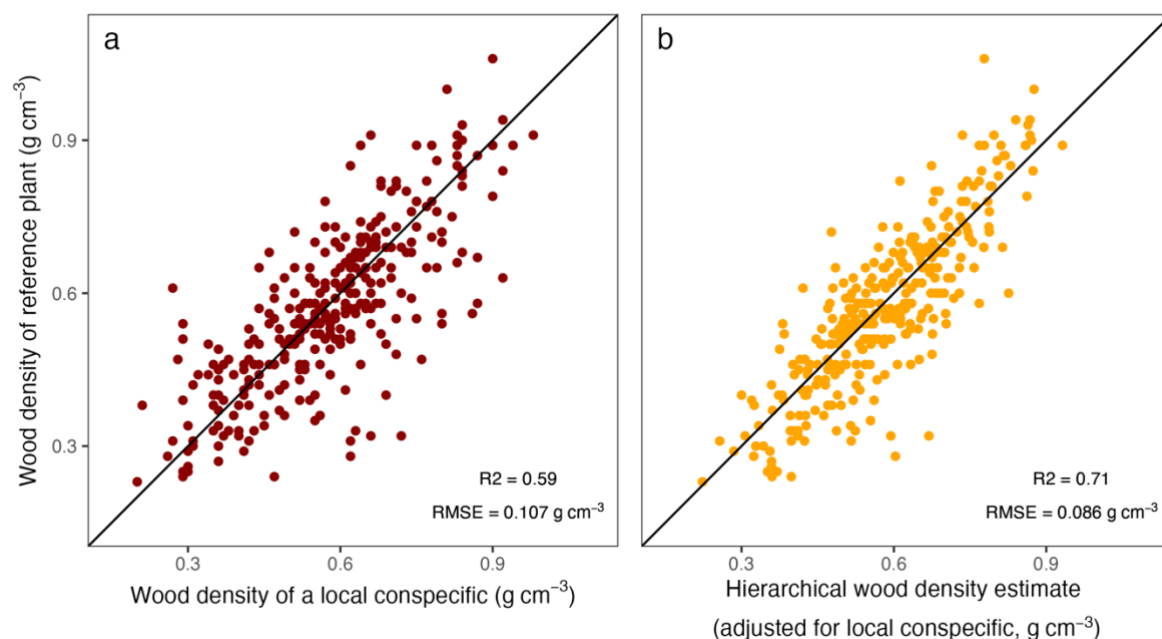
Fig. 4: Prediction of an individual plant's wood density from a local conspecific. Shown are two approaches to estimate an individual plant's wood density when a measurement from a local conspecific is available: a) using the conspecific's raw wood density measurement as an estimate, and b) using species or genus means adjusted by the local conspecific's value via hierarchical models (model M27, Table S3).

527 **4. Discussion**

528 Wood density is a key trait in plant ecology, acting as an indicator of species' competitive

529 abilities (Kunstler et al., 2016), demographic rates (Adler et al., 2014), and ecological

530 strategies (Chave et al., 2009; King et al., 2006; Kraft et al., 2010). The importance of species-

531 level differences in wood density is well-known (Phillips et al., 2019). However, intraspecific

532 variation is commonly considered less relevant due to the large amounts of wood density

533 variation explained by taxonomic and phylogenetic relationships (Chave et al., 2009), the

534 strong genetic control over wood density (Cornelius, 1994; Zobel & Jett, 1995) and a limited

535 contribution to community-level variation in comparison with other plant traits (Siefert et al.,

536 2015). Given that intraspecific variation in traits plays a crucial role for ecological processes

537 (Bolnick et al., 2011; Des Roches et al., 2018) and may influence biomass estimates (Momo et

538 al., 2020), we here re-examined this hypothesis at a global scale via the newly assembled

539 Global Wood Density Database v.2, which, compared to the previous version (Zanne et al.,

540 2009), included more than 6x as many records, more than doubled the number of species,

541 and added key information on sources of intraspecific variation.

542

543 *Intraspecific variation in wood density matters*

544 In the GWDD v.2, intraspecific variation in wood density (sd = 0.068 g cm^{-3}) was substantial

545 and structured according to both internal factors (within-plant structure) and external factors

546 (environment). Intraspecific variation accounted for up to 15% of global wood density

547 variation and followed predictable patterns with environmental factors. Wood density

548 increased with water deficit and more weakly decreased with soil pH. These results were

549 consistent across models and datasets (Table S10-13) and confirmed expectations that plants

550 with high wood densities should be favoured in extreme and nutrient-poor environments

551 (Anderegg et al., 2021; Gourlet-Fleury et al., 2011; Ibanez et al., 2017; Muller-Landau, 2004;

552 Yang et al., 2023). There was also a general trend of increases in wood density with

553 temperature, both in and out of the tropics, which may also reflect higher risks of drought-

554 induced embolisms in hotter environments, but it was not as clear as trends with water

555 availability (Tables S10-15). Crucially, environmental effects at intraspecific level were

556 strongly correlated with interspecific effects (r = 0.83) and were also consistent with a

557 companion study that found that community-means of wood density increased with

558 temperature and aridity (Fischer et al., submitted). This consistency of environmental effects

559 across scales was surprising, since previous studies found that variation in plant traits is often

560 shaped by scale-dependent physiological and ecological mechanisms (Anderegg et al., 2018;

561 Fajardo et al., 2024; Wang et al., 2022; Zhou et al., 2022). Wood density, with its genetic

562 limitations on variation, might thus be an exception, with similar physiological constraints

563 operating across different levels of ecological organization.

564 We also found that previously hypothesized patterns of variation in wood density

565 within individuals (MacFarlane, 2020; Woodcock & Shier, 2002) generalized to global scales.

566 Across species and studies, wood density varied less in sapwood than in heartwood and less

567 in branchwood than in trunkwood. Species with low-density heartwood had denser sapwood

568 and species with low-density trunkwood had denser branchwood, and vice versa in both cases

569 (Fig. 2a and b). An explanation for the heartwood-sapwood trends may lie in distinct

570 ecological strategies with changes in ontogeny (Hietz et al., 2013; Wiemann & Williamson,

571 1988; Woodcock & Shier, 2002), i.e., that some species tend to grow fast early in their life,

572 investing little in dense wood, but slow down in later life. The opposite strategy – investing

573 first in dense wood and then accelerating diameter growth later in life – has also been

574 suggested, but appears less common (Osazuwa-Peters et al., 2014). Trunk-branchwood

575   patterns have been explained through stronger functional constraints on branches than on

576   trunks (MacFarlane, 2020; Momo et al., 2020), but it has also been argued that they may be

577   explained by sapwood fractions (Gartner, 1995), since corewood formation at the tip of the

578   stem occurs at the same time as the formation of outer wood at its base (cf. summary in

579   Wiemann & Williamson, 2013). Indeed, when we compared only sapwood samples,

580   differences between branch and trunkwood largely disappeared (Fig. 2c). These results need

581   to be qualified, however. While we found clear global patterns, our findings relied on coarse,

582   binary distinctions between woody tissue types and thus glossed over methodological

583   differences between studies, as well as finer biological details. Changes in wood properties

584   from the pith to bark or from base of trunk to branches often follow non-linear patterns and

585   vary strongly between individual plants (Osazuwa-Peters et al., 2014; Schuldt et al., 2013;

586   Terrasse et al., 2021), both of which remain to be studied in future research.

587   Our study also demonstrated that intraspecific variation in wood density has

588   implications for applications such as carbon stock assessments or functional ecology. It is

589   common practice to use individual wood density measurements as estimates for species

590   means (Réjou-Méchain et al., 2017), but we found that individuals were generally so variable

591   that a species mean was less accurately estimated from a single species measurement than

592   from a genus mean. When applying hierarchical models, we found strong improvements in

593   predictive accuracy for species means (from RMSEs g cm^{-3} of 0.084 down to 0.038 g cm^{-3} with

594   two samples). However, increased sampling and hierarchical models did not help with

595   predicting an individual plant's wood density. Even from three samples of local conspecifics,

596   RMSEs did not decrease below 0.082 g cm^{-3}, indicating that there was substantial biological

597   variation among and within individuals that could not be explained by site-specific

598   environmental factors or phylogenetic relatedness. We note, however, that our study could

599   not examine the local growth conditions and competitive neighbourhood of individuals,

600   which likely play an important role in explaining intraspecific variation in wood density

601   (Kunstler et al., 2016).

602

603   *But intraspecific variation in wood density is also limited*

604   Despite the importance of intraspecific variation in wood density, we still found that its extent

605   was limited. First, it accounted for less of the total variance than taxonomic variation at

606   species (17%), genus (30%) or family (30%) levels. Second, average environmental effects and

607   gradients within individuals were generally small (usually ~0.01 g cm^{-3} or less, exceptionally

608   ~0.02 g cm^{-3}). They amounted to only 20-30% of species-level effects and were outweighed

609   both by methodological uncertainties, as may arise from differences in drying temperatures

610   or wood coring (estimated at sd = 0.049 g cm^{-3} when counting only between-study

611   differences, model M1, Table S4), and large among-species variation in the direction and

612   magnitude of intraspecific effects. For example, across species, we found an average decrease

613   of -0.023 g cm^{-3} from trunk to branchwood, but species varied in this relationship with sd =

614   0.075 (model M10, Table S8). This result means that branchwood density was still higher than

615   trunkwood density by more than 0.015 g cm^{-3} in ca. 30% of species. Similarly, despite an

616   intraspecific increase of wood density with water deficit of 0.010 g cm^{-3}, species varied in this

617   effect with sd = 0.038 g cm^{-3} (model M16, Table S10), meaning that in ca. 30% of species wood

618   density decreased with water deficit by a similarly-sized 0.010 g cm^{-3}.

619   It is possible that these estimates of variation in effect sizes were slightly too large,

620   since global collections such as the GWDD v.2 accumulate variation from many sources. Also,

621   they do not systematically sample across species' entire environmental ranges, meaning

622   errors across small environmental gradients and local growth conditions (light, rocks,

623   waterlogging) may introduce uncertainty. Some studies, for example, found that intraspecific

624   variation was better predicted when large aridity or temperature gradients were

625   systematically sampled (Anderegg et al., 2021). However, other studies with systematic

626   sampling designs did not find consistent effects of the environment on intraspecific variation

627   (Richardson et al., 2013; Rosas et al., 2019), and a replication of our analysis with a higher-

628   quality subset of the GWDD v.2 did not change the results: for example, we still found the

629   same small intraspecific increase with water deficit (0.008 g cm^{-3}), the same large variation

630   around this mean effect (sd = 0.039 g cm^{-3}), and the same much larger effect of 0.045 g cm^{-3}

631   among species (model M18, Table S10).

632   Overall, this large variability in effect size and direction indicated that intraspecific

633   wood density variation, even when following broad patterns, was difficult to predict. In

634   practice, the inclusion of the location of tissues (branch vs. trunk) into hierarchical models of

635   wood density variation improved predictions at the species level from RMSE = 0.043 to 0.038

636   g cm^{-3} (assuming two wood density measurements, Table S16), but impacts on individual

637   plant wood density estimates were minimal, with RMSE = 0.085 vs. 0.084 g cm^{-3} (also

638   assuming two wood density measurements, Table S17). These findings are consistent with

639   several previous studies which found clear patterns for community- and species-level wood

640   densities (Chave et al., 2009; Kraft et al., 2010; Swenson & Enquist, 2007) where errors were

641   smaller than total variation among taxa, but could not replicate these results at the

642   intraspecific level, with patterns seemingly unpredictable (Fajardo, 2018; Richardson et al.,

643   2013; Rosas et al., 2019; Umaña & Swenson, 2019).

644

645   *When to account for intraspecific variation in wood density: A tale of two scales*

646   Overall, our study showed that the decision of accounting for intraspecific variation in wood

647   density depends on the scale of the research question. Measuring each individual's wood

648   density and how it changes across its organs is paramount when studying plastic growth

649   responses in individual plants. Intraspecific variation of up to 0.068 g cm^{-3} meant that two

650   measurements of individuals from the same species could easily be separated by as much as

651    $\pm$0.19 g cm^{-3} (95% interval of the difference between two draws from a normal distribution

652   with sd = 0.068 g cm^{-3}). This variability should be large enough to overwhelm most species

653   differences at a single site and led to large errors when predicting an individual's wood

654   density, with R^2 as low as 0.59 and RMSEs as high as 0.108 g cm^{-3} in this study (Fig. 4).

655   Intraspecific variation in wood density may thus dominate species-level differences within

656   communities or even across communities if these are dominated by only a few species that

657   are close in average wood density values (cf. patterns in Anderegg et al., 2021). Another case

658   where intraspecific variation should be accounted for is the determination of individual tree

659   biomass from terrestrial laser scanning (TLS). TLS-derived 3D volumetric models can give

660   precise volume estimates (Calders et al., 2015), which then must be combined with wood

661   density to transfer volume to biomass. However, TLS estimates can be costly to construct, and

662   their volume estimate precision only matters if wood density variation among individuals and

663   along the hydraulic pathway are accounted for (Demol et al., 2021; Momo et al., 2020). Since

664   we found errors of at least 0.08 g cm^{-3} when predicting wood density at the individual tree

665   level (or between 10-20% of wood density, assuming most plants have densities between 0.40

666   and 0.80 g cm^{-3}), studies likely cannot infer this variation, but need to systematically sample

667   multiple individuals with at least two samples per measurement location.

668   By contrast, if the aim is to assess average community structure and vegetation

669   dynamics at large scales or across steep environmental gradients, it makes sense to prioritize

670   taxonomic coverage (Phillips et al., 2019) over the exhaustive sampling of individuals from a

671   single species. First, as we showed here, variation at species or higher taxonomic levles

672   accounted for most variation in wood density (77%). Second, environmental effects at the

673   intraspecific level aligned with interspecific effects (r = 0.83). Third, variation among and

674   within individuals within sites is expected to average out at the community level. Therefore,

675   as long as a wide range of communities is sampled, the omission of intraspecific effects should

676   not introduce systematic bias. In some cases, such as wood density predictions via machine

677   learning models (Yang et al., 2024), it may even make sense to ignore intraspecific information

678   on purpose, as the risk of overfitting or mistaking small methodological differences for

679   biological variation outweighs the benefits of small corrections of ~0.01 g cm^{-3} or less.

680   Similarly, intraspecific variation in wood density should play a minor role when applying pre-

681   calibrated allometric models to estimate tree biomass, as its variance is dwarfed by other

682   sources of uncertainty, such as allometric models and estimates of plant size and shape

683   (Chave et al., 2014; Kindermann et al., 2022; Molto et al., 2013; Réjou-Méchain et al., 2017).

684

685   *Global traits databases as backbones for hierarchical models*

686   A key takeaway of our study is that, no matter the level of analysis, wood density

687   measurements should not be treated as monolithic true values. Rather, they are noisy trait

688   estimates that can be refined by including prior information through shared evolutionary

689   history or measurement locations (Funk et al., 2017). Here, we applied simple hierarchical

690   models based on taxonomic relationships and found that they vastly outperformed simple

691   averaging procedures, particularly for undersampled species. A single wood density

692   measurement was as poor an approximation of the species mean as a genus mean that did

693   not involve any sampling of the target species (Tables S16), but errors decreased substantially

694   when combining both in a hierarchical model (Fig. 4, Tables S16-17). Approaches could be

695   further refined by explicitly accounting for phylogenetic relationships, but this approach

696   comes with its own challenges (Revell, 2010), and taxonomic hierarchies may provide a good

697   approximation (cf. https://statmodeling.stat.columbia.edu/2016/02/14/hierarchical-models-

698   for-phylogeny-heres-what-everyones-talking-about/, last accessed on 9 September, 2024).

699   Overall, our findings suggest that there is great value in open-access trait database

700   such as the GWDD v.2, as they synthesize knowledge across a range of disciplines and help

701   correct noisy local estimates. They also provide insights on ecological strategies, variation

702   across biogeographic realms, and, with careful curation and documentation (Augustine et al.,

703   2024), allow us to explore intraspecific variation. At the time of writing, version 1 of the GWDD

704   has been downloaded almost 20,000 times. Many of the applications of this database have

705   been in assessing forest carbon storage, in connection with REDD+ projects or carbon credit

706   accounting programs. As this sector is coming under closer scrutiny, reducing uncertainty in

707   carbon estimates is a timely ambition, and the GWDD v.2 will be an important contribution.

708   The findings in this study will also be helpful for developing theories about the evolution of

709   carbon investments in plants (Castorena et al., 2022), improving the parameterization of

710   global dynamic vegetation models, and providing guidance on how to account for intraspecific

711   variation in ecological studies. In the future, we hope that the openly available and thoroughly

712   documented GWDD v.2 will encourage the documentation and sharing of more wood density

713   datasets and the construction of similar databases for other traits.

714

715   **Acknowledgments**

766

767   Above all, we thank the work of thousands of anonymous trait collectors and wood

768   technicians; taxonomists who maintain and harmonize species records; foresters, ecologists,

769   students, and field assistants who measure woody plants on the ground; meteorologists who

770   man weather stations and collect climate data; satellite engineers, climate scientists and IT

771   developers who develop models and maps as well as the software to analyze them; as well as

772   individual citizens, local communities, and public and private bodies that support this work.

773

774   **Competing Interests**

775   None declared.

776

777   **Author contributions**

778   F.J. Fischer, J. Chave and A. Zanne conceived of the project. F.J. Fischer led the assembly and

779   processing of the database, the analysis for the manuscript, and the writing of a first draft of

780   the manuscript, with assistance from J. Chave, A. Zanne, T. Jucker, A. Fajardo, A. Fayolle, R.A.F.

781   de Lima and G. Vieilledent. All co-authors contributed substantially through data collection,

782   data assembly and revisions of the manuscript.

783

784   **Data availability**

785   The Global Wood Density Database v.2 and derived wood density estimates at species and

786   genus level will be made openly available in a dedicated Zenodo repository upon publication

787   (doi: 10.5281/zenodo.16919509). All other data and code underpinning the results of this

788   article are publicly archived in a separate Zenodo archive, which will also be publicly available

789   upon publication (doi: 10.5281/zenodo.16928343).

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