Variations in temperate forest stem biomass ratio along three environmental gradients are dominated by interspecific differences in wood density

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Abstract Stem biomass ratio (SBR, kg m$^{-3}$) is a forest state variable that converts forest volume of growing stock into biomass. However, huge intraspecific variation in wood density (WD) driven by biotic and abiotic environments of tree growth remains ignored in C budgets. The aims of this study were (i) to identify variations in SBR along water, soil nutrition and elevation gradients, (ii) to test for differences between broadleaved and conifer tree species in SBR variations, and (iii) to weight the contributions of interspecific and intraspecific diversity in SBR variations. Analyses were based on massive X-ray WD measurements performed on 54,700 tree cores collected in 2016 and 2017 on the spatially systematic plot sampling design of the French national forest inventory (NFI) programme. Stem biomass ratio (SBR) variations along the three gradients were found to be significant, with differences between botanical classes found on the water gradient only. SBR hence decreased by 73 kg m$^{-3}$ (conifers) and 126 kg m$^{-3}$ (broadleaves) along a 180 mm gradient of soil water holding capacity (SWHC), increased by 153 kg m$^{-3}$ along a full gradient of soil basicity index (SBI), and decreased by 155 kg m$^{-3}$ from 200 to 2000 m of elevation asl. Species distribution, not intraspecific variation in WD, was found to be the main cause of SBR variation along these gradients. SBR was found to be efficient for analysing large scale vegetation changes along environmental gradients, with interspecific variability being well explained by the three gradients. Mean WD species values were found to suffice to assess these SBR variations at the scale of the French forest resources.

Keywords Stem biomass ratio · Wood density · Environmental gradients · Interspecific · Intraspecific · National forest inventory

Abbreviations

SBR Stem biomass ratio
NFI National forest inventory
SWHC Soil water holding capacity
SBI Soil basicity index
WD Wood density
Introduction

The need to limit global warming to 1.5 °C (IPCC 2018) gives forests a major role to play in sequestering CO₂ (Pan et al. 2011) but this requires sound knowledge of the components of forest biomass. Stem biomass ratio (SBR) is the variable that allows for the conversion of a forest’s volume of growing stock into a forest’s biomass of growing stock and it therefore plays a key role in forest carbon accounting on a large scale (Kauppi et al. 2006). SBR is defined as the community-weighted mean of the basic wood density (WD), which is the oven-dry weight of the tree stem divided by its green volume (Glass and Zelinka 2010). Basic wood density is a standard desirable reference used for calculating forest biomass and for comparison between species (IPCC 2006, 2019: recommendations regarding biomass estimation have remained constant since 2006). Since both mass and volume depend on moisture content, the analysis of the WD variability from the literature needs to be done rigorously (Williamson and Wiemann 2010; Vieilledent et al. 2018). For convenience, we will use the generic expression ‘wood density’ or WD for both our measurements and for the results from the literature that reports on WD measured in various wood moisture contents.

Since carbon accounting is performed over wide territories, SBR has to be quantified over representative samples. In this respect, National Forest Inventories (NFI) have been implemented since the early twentieth century in Europe (Tomppo et al. 2010) in order to assess forest resources and their changes over time, including the estimation of tree volumes. They hence form a primary support for systematic sampling of forest areas and mensuration attributes of their growing trees, and should play an increased role in these quantifications.

Due to high additional costs, WD is not routinely measured by NFI programs. Therefore, biomass estimates rely on combining tree volumes from NFIs and at best one average WD value per species (IPCC 2006), or by using allometric biomass equations (Chave et al. 2004). These values are extracted from existing WD databases (Loustau et al. 2004; Dupouey 2002; Mathieu 1877 in France). In Europe, if WD values for some countries are not available, the IPCC 2006 recommendations are to use the WD values published by Dietz (1975). For other continents, several well-known WD databases have been published by Zanne et al. (2009), a global WD database by Chave et al. (2009), a North America database by Miles and Smith (2009), and an Africa database by Carsan et al. (2012). Also, despite their strong interest, the WD values from these databases are not representative of the large tree populations existing within different national forest resources containing variable growing conditions. The literature hence reports on the huge variability in WD, ranging from 100 to 1300 kg m⁻³ across tree species as inferred from the Wood Density Database (Zanne et al. 2009; Chave et al. 2009). While intraspecific variability is not accurately described in these databases, which are oriented toward trait analysis, intraspecific variation remain important. For instance, WD in *Picea abies* varies from 350 to 500 kg m⁻³ (Trendelenburg and Mayer-Wegelin 1955; Hakkila 1989) and from 650 to 850 kg m⁻³ e.g. in *Quercus petraea* (Bergès et al. 2000, 2008). Nonetheless, when this variation has been considered across contrasting biotic (Fajardo 2016) and abiotic (Fajardo 2018) conditions, WD varies little at the intraspecific level.

Availability of energy, water and nutrient resources is fundamental to forest ecosystem structure and function (Chapin et al. 1987; Reich et al. 2003). It also plays a role in the variability of WD across species and populations (nutrient and water resources in Chave et al. 2009; temperature in Beets et al. 2007 and Filipescu et al. 2014). At the same time, wide gradients in the abiotic environment determine tree species distribution (Hacke and Sperry 2001; Marksteijn et al. 2011; Reich 2014), making the respective influences of inter- and intraspecific variability on the SBR unclear, and prone to depending on spatial scale (Albert et al. 2011; Siefert et al. 2015). Their quantification is thus a key to deciding whether intraspecific variation can be ignored (Shipley et al. 2016). In tropical forests, studies have most often considered both sources of variation along elevation (Zhang and Yu 2018), soil nutrient richness (Liu et al. 2012; Missio et al. 2016; Zhang and Yu 2018), and water availability (Hacke and Sperry 2001; Preston et al. 2006; Marksteijn et al. 2011; Reich 2014; Terra et al. 2018). Nevertheless, few have examined respective contributions of intra- and interspecific variations to WD along these gradients. By contrast, much more emphasis has been placed on single-species studies of WD (e.g. in *Nothofagus pumilio* in Fajardo 2018;
Quercus petraea in Bergès et al. 2008; Pseudotsuga menziesii in Lassen and Okkonen 1969). The respective contributions of intra- and interspecific variation in WD to SBR changes along environmental gradients therefore still need investigation.

In this respect, French forests are located in contrasting geologic (acidic to calcareous) and climatic conditions (Rameau et al. 1989), with climates ranging from Mediterranean to continental. With over 150 forest tree species, specific diversity is also maximum in this country with respect to the European continent (Barbati et al. 2014; Bontemps et al. 2019). They also cover 30% of the French territory, at 16.7 million ha (IGN 2016), and therefore encompass 24% of Central-and West European forests, as defined by Forest Europe (2015). WD studies available over this territory are on monospecific stands and limited geographic areas of predominant tree species, including mainly Fagus sylvatica (Bouriaud et al. 2004; Bontemps et al. 2013), Quercus robur and petraea (Ackermann 1995; Guilley et al. 1999; Bergès et al. 2000), Picea abies (Bouriaud et al. 2005; Franceschini et al. 2012, 2013) or Pinus pinaster (Bouffier et al. 2008). In these publications, WD variation are usually explained by the ring width and ring age variations and sometimes by also including the effects of temperature and precipitation (Franceschini et al. 2013) or other site factors (Bergès et al. 2008). No reference describing interspecific variation in WD in Western European forests was identified, except for an ancient compilation of WD measurements (Mathieu 1877).

In a context where accounting for carbon remains a priority, a full retention of all tree cores routinely collected over the French forest territory by the NFI program (systematic survey design on the whole territory) was implemented. This was initiated in 2016 (Leban et al. 2016) in order to perform massive WD measurements with an X-ray medical scanner (Jacquin et al. 2019). The associated database used in this paper covers 125 tree species and includes 54,700 tree cores (Leban et al. 2020), making it possible to search for SBR responses across environmental gradients, and disentangle the respective contributions of inter- and intraspecific diversity to these responses. Coupled with the NFI information system, the SBR can be estimated over any stratum of these forests. Soil water holding capacity (SWHC) and soil basicity index (SBI), computed from NFI field measurements, were considered as proxies for water and nutrient resources.

Elevation as a proxy for temperature was also searched for in view of its wide gradient across the territory. Tree species diversity was described on the scales of both botanical class and tree species. Botanical classes distinguish conifer from broadleaved tree species. Botanical classes distinguish conifer from broadleaved tree species. Botanical classes distinguish conifer from broadleaved tree species. Botanical classes distinguish conifer from broadleaved tree species. Botanical classes distinguish conifer from broadleaved tree species. Botanical classes distinguish conifer from broadleaved tree species. Botanical classes distinguish conifer from broadleaved tree species. Botanical classes distinguish conifer from broadleaved tree species. Botanical classes distinguish conifer from broadleaved tree species. Botanical classes distinguish conifer from broadleaved tree species. Botanical classes distinguish conifer from broadleaved tree species. Botanical classes distinguish conifer from broadleaved tree species. Botanical classes distinguish conifer from broadleaved tree species. Botanical classes distinguish conifer from broadleaved tree species. Botanical classes distinguish conifer from broadleaved tree species.
Rodríguez et al. 2006) and interspecific levels (Wheeler and Baas 2018).

– (H3) Both interspecific and intraspecific variation in wood density are expected to significantly affect BR variation along the gradients due the geographical scale considered (Albert et al. 2011).

Methods

Data

Sampling and data collection

Tree cores routinely sampled during forest inventory operations in 2016 and 2017 of this continuous (annual) systematic sampling process (Robert et al. 2010; Hervé 2016) were collected for laboratory measurements. National Forest Inventory (NFI) core sampling was performed on the living trees selected for measurements (1 out of 2 living trees) on the 10,200 NFI plots covering the French metropolitan forests. Increment cores were extracted at a conventional 1.30 m height with increment borers (diameter 4.3 mm). In total, 54,700 increment cores were collected from 125 species, of which 66 species were sampled with more than 30 increment cores. About 32% of the cores were sampled from the bark to the pith (in order to estimate tree age), the rest of the cores having on average a length of 58% of the tree radius (see Supplementary material 1). Of note, while such data collection does not provide any information on vertical variation in WD along tree stems, this measurement effort in unprecedented because it is based on a statistically, systematic and representative sampling method covering the total French forest territory and describing all tree species and tree social ranks.

Sample processing

Core drying, X-ray measurements and computation of the average core density are detailed in Supplementary material 1. Basic data consist in wood density profiles at a 0.625 mm resolution, averaged over tree cores using the CARDEN software (Jacquin et al. 2019). The process led to obtaining estimates of the basic specific gravity of wood for effective conversion of green volume into dry biomass. It varied from 200 to 1080 kg m$^{-3}$ across the full sample, and from 372 kg m$^{-3}$ for Pinus strobus to 875 kg m$^{-3}$ for Quercus ilex, on average across species.

Imputation of wood density

To reduce NFI costs, increment cores were not sampled on all the trees measured on a forest inventory plot. On each NFI, at least two trees per species and per each of the five conventional DBH classes were selected (Supplementary material 1, IGN 2019) when possible. Thus, based on this pairing process, WD values were assigned to 94.5% of the living trees measured for size and without sampled cores (70,100). Other inventoried but non-cored trees (5.5%) that did not have a paired tree on the plots were therefore assigned a mean WD per tree species and diameter class.

Biomass ratio calculation

The stem biomass of a tree was computed using WD as described above (used as tree stem WD approximation) multiplied by the stem volume (fresh volume at an upper threshold diameter of 7 cm) estimated with NFI volume equations including as predictors the circumference at breast height, total height and first tree branching height (IGN 2018), i.e. the height where an abrupt change of diameter or form occurs. Total stem biomass and volume were calculated for each plot.

The SBR (kg m$^{-3}$) was defined as the ratio between biomass per hectare on a plot and the total volume per hectare on the same plot (see Supplementary material 1). Using the statistical weights of NFI plots, the SBR could then be computed for any forest entity defined by common attributes across plots.

Variables used for the analysis

Environmental indicators derived from NFI data collection included: (i) Soil water holding capacity (SWHC) at 1 m depth computed from soil depth, texture and stoniness (Baize and Jabiol 1995; Baize 1988) as a proxy for soil water availability, which ranged from 5 to 180 mm over the full sample, (ii) a plant bioindication of the soil basicity index (SBI) based on a vegetation survey as a proxy for cationic
elements availability (Rowley et al. 2018) varying from 1 (acid) to 11 (basic) (Rameau et al. 1989), and (iii) the elevation ranging from class 300 m (200 to 400 m) to over 2000 m, as a proxy for temperature, with a significant ($p < 10^{-4}$) correlation of $+0.7$ between elevation and mean annual temperature (see Supplementary material 2). Details on environmental indicators can be found in Supplementary material 3. The SBR results were split into two dominant botanical classes by applying a threshold of 50% of the canopy cover. If more than 50% of the canopy cover was obtained from broadleaved species, then the SBR value was labelled ‘Broadleaves’ and vice versa for ‘Conifers’.

Interspecific variability was assessed by using means of tree species WD and their average position over the gradients.

Analyses

The three environmental gradients were defined by ordinated categorical variables and treated as continuous variables. To quantify SBR variations along the three environmental gradients (Q1), we applied weighted linear regression, intended to account for sample size in the factor levels. To explore differences in these responses between conifer/broadleaved-dominated plots (Q2), weighted ANCOVA of the SBR against gradient and botanical class (broadleaves and conifers) were fitted. In addition, a multiple linear regression was performed between the SBR and the three gradients in order to confirm the direction and significance of the different effects evidenced.

Unless forest plots are monospecific (only half of the French NFI plots, Morneau et al. 2008), SBR as a plot metric cannot be used to accurately describe interspecific variability. Therefore, variations in WD between tree species across environmental gradients were searched for using species averages of WD. The relative importance of interspecific/intraspecific sources of variation in WD was measured by a one-way ANOVA of WD against tree species. Intra- and interspecific variability is illustrated in Table 1 for the main forest tree species (with more than 2000 cores each), five species with the highest average WD and another five with the lowest WD. Interspecific variation was measured by linear regression between mean species WD and their respective position along the gradient, weighted by the number of samples. Last, to test for the influence and significance of intra-specific variability in WD on SBR responses, we calculated the SBR with two different methods: SBRm by using for each tree the species means of WD, to be compared to the initial SBR defined above and here named SBRi, which is computed with one individual WD value per tree. The method (SBRi or SBRm) was treated as a categorical variable in the statistical model. Weighted analyses of covariance (ANCOVA) of the SBR against each environmental gradient and the estimation method (SBRi and SBRm, in their additive or interactive form) were then fitted to explore systematic method-driven differences in the SBR along these gradients. To quantify the intraspecific effects on the SBR as a community trait, we used the method described in Lepš et al. (2011) intended to quantify species turnover and intraspecific variability effects on SBR variations.

Data were analysed using R software (R Development Core Team 2011).

Results

SBR variations along the three gradients and difference between broadleaves and conifers (Q1 and Q2)

The SBR varied between 287 and 1010 kg m$^{-3}$ across NFI plots. Mean SBR for broadleaf-(respectively conifer-) dominated plots was 582 kg m$^{-3}$ (respectively 433 kg m$^{-3}$). We tested Pearson’s correlations between the different gradients using values from each plot. The correlations were null (between the SBI and elevation, $p = 0.28$) to weakly negative between SWHC and the SBI ($-0.14$, $p < 10^{-4}$, $R^2 = 0.02$), and negative between SWHC and elevation ($-0.29$, $p < 10^{-4}$, $R^2 = 0.08$).

Along the SWHC gradient, the SBR varied from 710 to 580 kg m$^{-3}$ (resp. from 480 to 410 kg m$^{-3}$) for broadleaf- (resp. conifer-, Fig. 1a) dominated plots. The average gradient across all plots amounted to $-77$ kg m$^{-3}$ ($-12\%$), and was found to be non-significant ($p = 0.15$, $R^2 = 0.24$, H1.1). The covariance analysis confirmed a weak interaction between the botanical class and this response, indicating a greater variation in SBR along the SWHC gradient within broadleaf-dominated plots ($p = 0.06$, $R^2 = 0.93$, H2). When this response was split by
botanical class, its intensity became significant with −0.56 kg/m³/mm for broadleaves ($p < 10^{-3}$), and −0.23 kg/m³/mm for conifers ($p < 10^{-2}$).

Along the SBI gradient, the SBR increased and varied from 580 kg m⁻³ (SBI class 1) to 690 kg/m³ (SBI class 10) in broadleaves, and from 440 to 510 kg m⁻³ in conifers (Fig. 1b), with an average increase by 153 kg m⁻³ (32%) over the gradient ($p < 10^{-3}$, $R^2 = 0.8$, H1.2). The covariance analysis showed an absence of interaction with the botanical class ($p = 0.71$, $R^2 = 0.96$, H2).

Along the elevation gradient, the SBR was found to decrease on average from 617 to 462 kg m⁻³ (25%), corresponding to a magnitude of +13 kg/m³/100 m elevation ($p < 10^{-4}$, $R^2 = 0.98$, H1.3). In broadleaves (resp. conifers), it ranged from 630 to 550 kg m⁻³ (resp. 490 to 420 kg m⁻³) at 1800 m elevation (Fig. 1c) (extreme deviations due to very few plots). The covariance analysis again showed a non-significant interaction with the botanical class ($p = 0.69$, $R^2 = 0.99$, H2).

The joint variation of the SBR along the three gradients was tested by a multiple linear regression model taking into account the interaction detected between SWHC and botanical class. The three effects and the interaction were found simultaneously significant and confirmed the possibility to disentangle their effects on the SBR.

Effects of intraspecific and interspecific variations in WD on SBR gradients (Q3)

**Interspecific variation in WD along the environmental gradients**

**SWHC.** Species means of WD showed a significant negative relationship ($−2.37 \text{ kg/m}^3/\text{mm SWHC}$, $p < 10^{-4}$, $R^2 = 0.67$) with SWHC (Fig. 2a), for both broadleaves and conifers, and consistent with SBR variation along the gradient (Fig. 1a).

**SBI.** Along the SBI gradient (Fig. 2b), mean WD revealed a significant positive relationship (11.62 kg/m³/unity of the SBI, $p < 0.05$, $R^2 = 0.55$), with greater WD located on more basic soils on average, consistent with SBR variation along the SBI (Fig. 1b).

**Elevation.** A non-significant negative cross-species relationship between mean WD and mean elevation was found ($−0.04 \text{ kg/m}^3/m$, $p = 0.21$, $R^2 = 0.53$) (Fig. 2c).

| Botanical divisions | Tree species | Average (kg m⁻³) | Standard deviation (kg m⁻³) | Confidence interval 95% | Coefficient of variation | Sample size |
|---------------------|-------------|------------------|---------------------------|------------------------|-------------------------|-------------|
| Broadleaves         | *Quercus pubescens* | 721 | 75 | 574–868 | 0.10 | 2738 |
|                     | *Quercus petraea* | 645 | 71 | 506–784 | 0.11 | 5397 |
|                     | *Quercus robur* | 626 | 67 | 495–757 | 0.11 | 6419 |
|                     | *Carpinus betulus* | 622 | 41 | 542–702 | 0.07 | 3737 |
|                     | *Fagus sylvatica* | 608 | 46 | 518–698 | 0.08 | 5376 |
|                     | *Fraxinus excelsior* | 597 | 57 | 485–709 | 0.10 | 2439 |
|                     | *Castanea sativa* | 503 | 57 | 391–615 | 0.11 | 2699 |
| Conifers            | *Pinus sylvestris* | 461 | 60 | 343–579 | 0.13 | 2446 |
|                     | *Abies alba* | 415 | 48 | 321–509 | 0.12 | 2620 |
|                     | *Picea abies* | 386 | 47 | 294–478 | 0.12 | 2503 |

The number of cores is proportional to the volume occupied by the species in the forests resources.

Table 1: Range of variation for basic specific gravity for the 10 main French forest tree species.

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**Note:** This is a partial transcription of a scientific document. The full context and comprehensive understanding are necessary to interpret the results accurately. The table provides specific gravity ranges for different tree species in the French forests, highlighting variability across different botanical classes and environmental gradients.
Fig. 1 Relationships between SBR and a SWHC, b SBI, and c elevation in the French forests. SWHC in mm, SBI on a scale from 1 to 11, Elevation in meters (dashed lines are used when there is not interaction between gradients and botanical divisions).

Fig. 2 Tree species mean position along the gradients of a SWHC, b SBI and c elevation. 125 species were investigated: 91 broadleaves and 34 conifers.
Sensitivity of SBR to intraspecific variability in WD along the gradients

A one-way ANOVA of WD against tree species showed that interspecific variation predominated over intraspecific variation across the 125 species ($R^2 = 73\%$). For the 10 most sampled tree species, the coefficient of variation of WD varied from 7 to 13\%, with a comparable order of magnitude across tree species (Table 1).

The sensitivity of SBR estimation to intraspecific variability in WD was systematically checked for. The effect of the estimation method (SBRi and SBRm) was tested in both regression models, under its additive and interactive forms. Whatever the gradient (Fig. 3), no systematic deviation between the two methods was evidenced (Table 2, H3). To quantify the contribution of intraspecific variation on the SBR along the three gradients, we used the method developed in Leps et al. (2011). We used SBRi where both intraspecific and interspecific effects are taken into account, and SBRm where only the interspecific source of variation is represented. The relative contribution of each influence in the variance can be found in Table 3. We found that the influence of intraspecific variation on SBR amounted to 1.5\% for SWHC, 2.0\% for the SBI and 0.7\% for elevation, in agreement with our findings on the predominant contribution of interspecific variability on SBR variations (H3). As a conclusion, even if we account for intraspecific variation in WD in SBR estimations this has no effect on their grand averages, and their variations along the three gradients.

Discussion

SBR variations along the three gradients (Q1) and differences between broadleaves and conifers (Q2)

We showed that the SBR decreased significantly with SWHC for both broadleaf- and conifer-dominated plots (Fig. 1a, H1.1). This pattern was consistent with the reported positive trait association of drought tolerance with species WD that affects SBR variation. This relationship has been mainly studied in tropical and subtropical forests (Hacke and Sperry 2001; Preston et al. 2006; Markesteijn et al. 2011; Reich

Fig. 3 Relationships between SBRi/SBRm and the three environmental gradients under study. a SWHC in mm, b SBI on a scale from 1 to 11, c elevation in meters
2014; Terra et al. 2018), with resistance to cavitation in drier conditions implying lower lumen size and greater WD (Preston et al. 2006). However, few studies have been carried out in temperate forests (Zanne et al. 2006; Hoffmann et al. 2011) where seasonality and different anatomical features (smaller conduit diameter in diffuse porous and ring-porous species) are specific to this environment (McCulloh et al. 2010). No study on the relationship between WD and drought tolerance was found for European species at the interspecific and intraspecific levels. Therefore, the finding that the relationship between the SBR and SWHC gradient is more intense (greater slope) in broadleaves is an original result of this study (H2). This result could be explained by forest compositional changes along the SWHC gradients, with more broadleaved tree species than conifers in dryer areas. However, on the contrary we found that the proportion of broadleaved tree species increased with SWHC from 72% with SWHC under 10 mm to 82% with SWHC above 170 mm. On the other hand this difference in slope intensity supports the idea that a more plastic wood anatomy leads to gradient-driven acclimation processes (Martínez-Cabrera et al. 2017).

The SBR showed a significant increase along the SBI gradient (Fig. 1b, H1.2). Very few studies have explored the impact of soil acidity on WD among and within tree species that may affect SBR variation. Liu et al. (2012) found a decreasing trend in WD with increasing soil acidity. While no study provides an interpretation for this reported effect on WD, soil acidity is known to impact nutrient concentration in the soil, in particular in Ca and Mg concentrations (van der Heijden et al. 2011; Jonard et al. 2012; Rowley et al. 2018), which are essential to photosynthesis (Masuda 2008) and wood structure (Ca ensures cationic bounds with pectin molecules in the cellular wall; Grant et al. 1973). Reduction in these nutrients’ availability may thus affect wood formation and WD. Furthermore, the relationship between WD and tree growth is usually negative (Drew et al. 2011; Pretzsch et al. 2018) and soil acidity has a negative effect on growth (fewer nutrients available). This can be evidenced in NFI statistics of volume production where this variable decreases with acidity for both broadleaf- and conifer-dominated plots from 5.5 (at 5 SBI) to 4.3 (at 1 SBI) m³/ha/year for the first one, and from 10.3 (at 5 SBI) to 6.7 (at 1 SBI) m³/ha/year for the second. Therefore, a decrease—not an increase—of the SBR with the SBI should be expected, contrary to what was found. Hence growth is not likely to account for SBR variation along the SBI. The universality of

### Table 2
Regression models of Stem Biomass Ratio against the three gradients with testing the effect of SBR estimation method (SBRi and SBRm)

| Regression model | SWHC       | SBI        | Elevation          |
|-----------------|------------|------------|--------------------|
| Gradient × methods | No interaction ($p = 0.77$, $R^2 = 0.20$) | No interaction ($p = 0.83$, $R^2 = 0.79$) | No interaction ($p = 0.57$, $R^2 = 0.98$) |
| Gradient + methods | No methods effect ($p = 0.88$, $R^2 = 0.20$) | No methods effect ($p = 0.85$, $R^2 = 0.79$) | No methods effect ($p = 0.90$, $R^2 = 0.98$) |

### Table 3
Disentangling of species turnover and intraspecific trait variability effects on SBRi, the relative contribution in calculated on the gradient effects on SBR

| Gradient | Turnover effect | Intraspecific effect | Covariation | Total |
|----------|----------------|---------------------|-------------|-------|
| SWHC     | Sum of squares  | 2309.1              | 43,998      | 637.48| 2990.5 |
|          | Relative contribution on gradient effect | 77%              | 1.5%        | 21%   | – |
| SBI      | Sum of squares  | 9101,1              | 244.71      | 2984.731| 12330.6 |
|          | Relative contribution on gradient effect | 74%              | 2.0%        | 24%   | – |
| Elevation| Sum of squares  | 16512.37            | 130.479     | 2935.654| 19578.5 |
|          | Relative contribution on gradient effect | 84%              | 0.7%        | 15%   | – |
wood chemical composition (Savidge 2008) may account for the absence of a difference in the SBR between broadleaves and conifers (H2).

We found a significant decrease in the SBR with elevation (Fig. 1c, H1.3). In Mankou et al. 2017, species mean WD was analysed over a more restricted gradient (500 to 1000 m) and showed a decrease with elevation at the interspecific level similarly to our results (Fig. 2). The slight increase at the end of the gradient (Fig. 1) could be explained by species with greater WD (i.e. *Larix decidua* for conifers), due to a narrower conduit diameter (Preston et al. 2006), to avoid freezing-induced cavitation (Hacke and Sperry 2001; Davis et al. 1999).

Interspecific variation in WD along the environmental gradients (Q3)

**Water gradient**

In tropical forests, the interspecific variation in WD was explained as an adaptation to drought conditions (Hacke and Sperry 2001). To test for this relationship, we looked at the correlation between species drought tolerance index (Niinemets and Valladares 2006) and WD, which was found to be significant (Table 4). The correlation between drought tolerance index and SWHC of each species was also significant, showing that species distribution across the study territory was in accordance with knowledge on their average ecological preferences.

**Soil richness in cationic elements gradient**

Along the SBI gradient, WD was found to increase across species, a relationship consistent with other studies (e.g. Liu et al. 2012). A significant correlation (Table 4, *p < 10^-4*) was found between acidity preference (functional trait from the ECOPLANT database, Gégout et al. 2005) and WD, which was consistent with our findings regarding species distribution along the SBI gradient. We also found a significant and consistent correlation between this functional trait and the SBI of each species.

**Elevation gradient**

At the interspecific level, we found a decrease in WD with elevation, which is consistent with other studies (e.g. Mankou et al. 2017). We found a significant (*p < 10^-4*) correlation of + 0.7 between elevation and mean annual temperature (see Supplementary material 2), making elevation a good indicator for temperature variation. To test for the possible effect of colder temperatures on interspecific variation of WD, we used a cold tolerance index (from 0 to 5) as a functional trait for each species, which is based on yearly minimum temperature of species habitat (Laanisto and Niinemets 2015). We found a weak correlation (Table 4) between cold tolerance and WD, and a non-significant one between cold tolerance and the mean elevation of each species. Therefore cold tolerance cannot explain interspecific variation of WD. To better understand why the WD trend is negative, additional analyses are necessary on a more focused scale, for instance, at the tree and species level for wood anatomical measurements, tracheid lumens, occurrence of compression wood, tree ages and size. These investigations may be possible on the sample, as all the selected cores remained stored.

Of note, Interspecific WD variability does not seem to be reduced at the extremities of any of the gradients under study.

Given the strong relationships between tree species averages of WD and environmental gradients, and the stronger effect of interspecific over intraspecific Table 4 Correlation between functional traits and wood density, and between functional trait and the gradients

| Gradient               | SBR—gradients relationships | Functional trait associated      | Functional trait—wood density | Functional trait—gradients |
|------------------------|-----------------------------|---------------------------------|-------------------------------|----------------------------|
| SWHC                   | −                           | Drought tolerance (Niinemets and Valladares) | 0,45***                      | − 0,41***                  |
| SBI                    | +                           | Acidity preference (Gégout et al.) | 0,29*                        | 0,66***                    |
| Elevation              | −                           | Cold tolerance (Laanisto and Niinemets) | − 0,19(*)                   | 0,13                       |

*p < 0.05, **p < 0.01, ***p < 0.001

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variability, the SBR could be predicted and used in large-scale vegetation models (Friend et al. 2019) and applied on forest growth to obtain forest productivity in biomass.

Sensitivity of SBR to intraspecific variability in WD along the gradients (Q3)

We found that the computed SBR with tree species means of WD (SBRm, Fig. 3) yielded the same SBR estimates (Table 2) as those computed with individual tree core measurements (SBRi). In this sense, intraspecific variability in WD did not influence the SBR, which is driven by the range of variation of the interspecific variability (H3). These results confirm the theory of Albert et al. (2011) on interspecific variability becoming more important than intraspecific variability with increasing spatial scale. On the contrary, intraspecific variability (Table 1) was much greater than that accounted for by the gradients (data not presented, $R^2 = 2.7\%$ on average on the three gradients, and ranging from 0.2 to 9.5%). It explains why intraspecific variability in wood density (confidence interval of 95%) is similar to or greater than (Table 1) SBR range over the gradients, but does not have any impact on SBR variation, this intraspecific variation of WD being unrelated to these environmental gradients. This suggested that other effects, including tree developmental stage (Franceschini et al. 2013; Guilley et al. 2004), micro-climate and genetics, and not captured in this study, may have a strong influence on this variability. This intraspecific variability has a key role when it comes to species adaptation and evolution (Albert et al. 2011). Species distribution over a gradient was found in strong accordance with its environmental preferences (Shipley et al. 2016), with greater abundance in one position on the gradient where species fitness is at its best. This finding echoes questions raised by Shipley et al. (2016): ‘When can intraspecific trait variation be safely ignored and when must it be included? For which traits is this true? Along which environmental gradients?’ WD has been previously identified as a conservative plant trait, with limited intraspecific variation on a large scale (Siefert et al. 2015) compared to other functional traits. On the contrary, specific leaf area, for example, has been described as far more variable at the intraspecific level (Shipley 2000; Fajardo and Piper 2011), and may not need the same treatment in ecological analysis.

With ongoing climate change yielding warmer and drier climates, a change in the SBR would also primarily result from shifts in plant community structure, i.e. changes in abundance or position of tree species along the gradients of SWHC and elevation. Due to the negative relationships evidenced between the SBR and water and elevation gradients, greater SBR are anticipated to be encountered in a warmer and drier future. What the extent of such increase may be and whether declines in tree growth (as already detected in France, Charru et al. 2017) would offset this increase have yet to be determined. Such results pave the way for new stimulating research questions and the possible use of SBR in large-scale forest productivity models.

Material limitations

This study was the first to re-use increment cores collected extensively over a wide forest territory by an NFI program and is, as such, unprecedented. This therefore comes with some issues in the methodology with respect to standards of the literature. A first methodological issue concerns the possible wood compaction resulting from the use of increment borers (Williamson and Wiemann 2010). The increment borers used had a diameter of 4.3 mm and were supposed to generate more wood compaction than a larger one (e.g. 12 mm, Williamson and Wiemann 2010). The measurement of wood properties on increment cores was initially performed for the measurement of growth stresses in standing trees (Polge and Thiercelin 1979) and also for doing anatomical measurements of the tracheid fibres and vessels (Gärtner and Nievergelt 2010). These analyses have shown that (i) green wood cores remain elastic with no plastic deformation (without compaction) and (ii) the borer does not alter the wood anatomical structure. It is of course necessary to use well-sharpened increment borers and to insert the borer in the trees without the borer moving about the central axis of the core. The growth stresses can be measured safely on tree cores (Wilkins and Bamber 1986), as well as WD.

As a second issue, WD variation along tree stems has been reported for several species (Wassenberg et al. 2015; Repola 2006; Billard et al. 2020), and was not considered in this study. Again, NFI-scale collection of wood material never includes tree samples at

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heights other than the conventional 1.30 m, therefore interactions between architecture, growth and wood density from the aerial parts and the crown of the tree remain out of scope of the present study. Also, both increasing and decreasing trends between WD and tree height have been reported in the literature (Wassenberg et al. 2015; Repola 2006). The effects of these variations on the biomass need to be evaluated, including the subsidiary tree social status effect, which depends on tree height. The outcome of an overestimation or an underestimation is therefore uncertain as this WD variability with height has been evaluated on small samples in very restricted species sets, and this therefore forms a true open research question.

It is also important to take into account that dimensional variations (for example height variation) affect both biomass calculation and volume calculation, thus the SBR based on stem biomass divided by the stem volume does not have a great sensitivity to these variations.

Conclusions

Analysed variations in the SBR across gradients of water and nutrient availability and elevation in temperate forests of Western Europe yielded the following main conclusions:

- For both broadleaf- and conifer-dominated plots, we found significant relationships between the SBR and water (−), soil richness (+) and elevation (−) gradients.
- The intensity of this relationship along the water gradient differed between broadleaves and conifers, but was found to be similar for the elevation and soil richness gradients.
- SBR gradients were strongly structured by tree species distribution; those with greatest/lowest SBR occupied opposing positions on any of these environmental gradients. Species distributions were found to be correlated with their quantified adaptation to water, temperature and mineral availability.
- Calculation of the SBR along these three gradients and on the scale of all French forests can be safely obtained by accounting for the interspecific WD differences only.
- Further research is needed to assess the impact of tree height sampling on SBR variation.

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Author contributions BK did the analysis. BK, JDB and JML wrote the manuscript. JDB and JML supervised the research carried out by BK for his PhD.

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Availability of data and materials The dataset used for this paper is available on the data INRAE repository and should be cited as follow: Leban, J.M., Kerfriden, B., Jacquin, P., Lacarin, M., Taupin, A., Mola, C., Duprez, C., Chabot S., Dauffy, V., Morneau F., Wurpillot, S., Hervé, J. C., 2020, “Wood basic density for 125 tree forest species from the French forests”, https://doi.org/10.15454/XFOPPL1. Part of these data are in the supplementary material.

Compliance with ethical standards

Conflict of interest The authors declare that they have no competing interests.

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