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► **To cite this version:**

Andrés González-Melo, Juan Manuel Posada, Jacques Beauchêne, Romain Lehnebach, Sébastien Levionnois, et al.. Radial variations in wood functional traits in a rain forest from eastern Amazonia. *Trees - Structure and Function*, 2022, 36, pp.569-581. 10.1007/s00468-021-02229-1 . hal-03456796

**HAL Id: hal-03456796**

**<https://hal.science/hal-03456796v1>**

Submitted on 30 Nov 2021

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1 Original article

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3 **RADIAL VARIATIONS IN WOOD FUNCTIONAL TRAITS IN A RAIN FOREST FROM EASTERN**  
4 **AMAZONIA**

5

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26 **Declarations**

27

28 Funding: The authors acknowledge financial support from Colciencias (Colombian Agency for Science and  
29 Technology) and the University of Guyane.

30 Conflict of interest: The authors have no conflicts of interest to declare.

31 Availability of data: The datasets analyzed during the current study are available in the OSF repository,

32 [ DOI 10.17605/OSF.IO/HS3MA]

33 Code availability: No

34 Authors' contributions: The study was designed by A.G.M., J.M.P., B.C. and J.B. Most wood samples were  
35 collected by R.L. and A.G.M. Additional samples were provided by B.C., J.B. and S.L. Anatomical images  
36 were processed by A.G.M. and K.R. Data analyses were performed by A.G.M. with contributions from J.M.P.  
37 The first draft of the manuscript was written by A.G.M. with inputs from J.M.P. All authors contributed equally  
38 to the writing and interpretation of advanced versions of the manuscript.

39 Ethics approval: Not required

40 Consent to participate: Not required

41 Consent for publication: Not required

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43 **Key message:** Positive radial trends in WSG were common among light-demanding species, and were mainly  
44 explained by radial shift in fiber and parenchyma traits.

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62 **ABSTRACT**

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64 Trees can modify their wood structure in response to changes in mechanical, hydraulic and storage demands  
65 during their life-cycles. Thus, examining radial variations in wood traits is important to expand our knowledge  
66 of tree functioning and species ecological strategies. Yet, several aspects of radial changes in wood functional  
67 traits are still poorly understood, especially in angiosperm trees from tropical humid forests.

68

69 Here, we examined radial shifts in wood traits in trunks of tropical forest species and explored their potential  
70 ecological implications. We first examined radial variations in wood specific gravity (WSG). Then, we asked  
71 what anatomical traits drove radial variations in WSG, and whether WSG, vessel fraction and specific hydraulic  
72 conductivity vary independently from each other along the radius gradients.

73

74 We measured WSG and eight wood anatomical traits, at different radial positions along the trunks, in 19 tree  
75 species with contrasting shade-tolerance from a lowland tropical forest in Eastern Amazonia.

76

77 Most species had significant radials shifts in WSG. Positive radial gradients in WSG (i.e., increments from pith  
78 to bark) were common among shade-intolerant species and were explained by different combinations of fiber  
79 and parenchyma traits, while negative radial shifts in WSG (e.g., decreases towards the bark) were present in  
80 shade-tolerants, but were generally weakly related to anatomical traits. We also found that, in general, WSG  
81 was unrelated to vessel fraction and specific hydraulic conductivity in any radial position.

82

83 This study illustrates the contrasting radial variations in wood functional traits that occur in tree species from a  
84 humid lowland tropical forest. In particular, our results provide valuable insights into the anatomical traits  
85 driving WSG variations during tree development. These insights are important to expand our knowledge on  
86 tree ecological strategies by providing evidence on how wood allocation varies as trees grow, which in turn can  
87 be useful in studying trait-demography associations, and in estimating tree above-ground biomass.

88

89 **Key words:** Wood functional traits, radial variation, tree functioning, tropical trees, wood anatomy.

## 90 INTRODUCTION

91

92 The study of wood traits has a long tradition in wood technology and wood anatomy (e.g., Zobel and Buijtenen  
93 1987, Carlquist 2001, Baas et al., 2016). Yet, with the emergence of trait-based ecology in the last decades  
94 (Westoby and Wright 2006, Shipley et al., 2016), there has also been an increasing interest in studying wood  
95 traits from an ecological perspective (i.e., Larjavaara and Muller-Landau 2010, Beeckman et al., 2016). One  
96 basic assumption of trait-based ecology is that, in broad interspecific comparisons, trait variation among species  
97 would be greater than among or within-individual trait variations (Shipley et al., 2016). Hence, most trait-based  
98 studies on wood have used mean trait values per species, overlooking the often remarkable trait variation that  
99 exists within trees (*i.e.*, Hietz et al., 2013, Olson and Rosell, 2013). As a consequence, several aspects of radial  
100 (*i.e.*, from pith to bark) changes in wood traits in individual trees, and their ecological significance, are still  
101 poorly understood (Lachenbruch et al., 2011, Hietz et al., 2016, Rungwattana and Hietz 2017). In this sense,  
102 studying these radial changes in wood traits may increase our understanding of stem allocation patterns and  
103 functioning during tree development, and consequently of life-history variations across species.

104

105 Wood specific gravity (WSG) is considered a central trait to understand tree functioning and species  
106 ecological strategies (Westoby and Wright 2006, Chave et al., 2009). For instance, WSG is generally related to  
107 biomechanical (King et al., 2006, Anten and Shieving 2010) or hydraulic properties (Santiago et al., 2004,  
108 2018), and is hypothesized to mediate a trade-off between stem construction and maintenance costs (Larjavaara  
109 and Muller-Landau 2010). Moreover, it is well established that there can be important radial changes in WSG  
110 within trees (Hietz et al., 2013, Osazuwa-Peters et al., 2014, Plourde et al., 2015). These radial trends in WSG  
111 may reflect the combined effects of the age of the vascular cambium, which can determine the size of wood  
112 cells produced (Lachenbruch et al., 2011), or tree diameter, since trees adjust their wood anatomy in response  
113 to size-related changes in mechanical and hydraulic demands (Nock et al., 2009, Williamson and Wiemann  
114 2010a, Rungwattana & Hietz 2017). Alternatively, these radial changes might be a consequence of the  
115 deposition of wood extractives in the inner wood during heartwood formation (Lehnebach et al., 2019, but see  
116 Larjavaara and Muller-Landau 2010).

117

118           In angiosperms, wood is composed of three main cell types: fibers that mainly provide mechanical  
119 support, vessels responsible for sap transport, and living parenchyma cells that, among others, store and  
120 transport nutrients and secondary metabolites (i.e., Carlquist 2001). As specific gravity (SG) is an emergent  
121 property of wood that is affected by the relative amount of fibers, vessels and parenchyma cells, quantifying  
122 radial shifts in their proportions and morphologies can help us attain a broader and deeper understanding of the  
123 functional bases underlying radial trends in WSG (i.e., Ziemska et al., 2015). A number of studies have  
124 examined the anatomical drivers of interspecific variations in WSG of angiosperm trees. These studies have  
125 shown that WSG can be driven by fiber traits such as fiber fraction or wall thickness (i.e., Martínez-Cabrera *et*  
126 *al.*, 2009, Fortunel *et al.*, 2013, Ziemska et al., 2013). Yet, this trend may not always hold for all species,  
127 especially for species with intermediate (*c.* 0.50-0.80) WSG, since some species with similar values of WSG  
128 may have contrasting wood anatomies (Ziemska et al., 2015).

129

130           Studies aiming at understanding the anatomical bases of radial changes in WSG have been mostly done  
131 on temperate gymnosperm species (reviewed by Lachenbruch et al., 2011), while very few studies have been  
132 conducted on tropical angiosperm forest trees (e.g., McDonald et al., 1995, Rungwattana & Hietz 2017). In one  
133 of these few studies, Rungwattana & Hietz (2017) showed that the anatomical drivers of radial shifts in WSG  
134 varied substantially among five tree species from a dry tropical forest. Yet, these results cannot be easily  
135 extrapolated to other tropical forests. First, radial variations in WSG are thought to be less pronounced in trees  
136 from dry forests compared to trees from humid forests, possibly because canopy stratification and light  
137 competition tend to be lower in dry forests (Wiemann & Williamson 1989). Second, WSG tend to be higher in  
138 dry forests than in humid ones (Chave et al., 2009), suggesting that in dry forest wood a large stem cross-  
139 sectional area is occupied by fibers. Third, trees from dryland areas also tend to have higher total parenchyma  
140 fractions than trees from humid areas (Morris et al., 2016). Thus, it is likely that radial gradients in wood traits  
141 reported for dry forest trees may differ considerably from those of humid forest trees. Despite the existence of  
142 valuable studies on WSG (i.e., Nock et al., 2009, Williamson and Wiemann 2010a, Hietz et al., 2013, Plourde  
143 et al., 2015) and vessel lumen size (i.e., Olson et al., 2013, Hietz *et al.*, 2016), detailed aspects of radial  
144 variations in wood traits in trees from humid tropical forests are still unknown.

145

146           An additional aspect to consider when studying the underlying anatomical drivers of radial changes in  
147 WSG is that, while WSG and fiber traits represent one major axis of variation in wood structure (Martínez-  
148 Cabrera et al., 2009, Fortunel et al., 2013, Zieminska et al., 2013), there is also substantial anatomical variation  
149 that is independent of WSG (Zieminska et al., 2015). For example, vessel fraction ( $F_V$ ), i.e., the amount of stem  
150 cross-sectional area allocated to vessels, is thought to reflect an axis of variation in xylem structure that is  
151 largely orthogonal to WSG (i.e., Zanne et al., 2010). This independence between traits may be significant  
152 because it suggests that hydraulic and mechanical functions might be decoupled (Hietz et al., 2016). There are  
153 good biophysical and anatomical reasons why these functions should be independent. For example, since  
154 specific hydraulic conductivity ( $K_S$ ) increases exponentially with vessel lumen area ( $V_A$ , Tyree and Zimmerman  
155 2002), trees may adjust  $K_S$  by small increments in  $V_A$ , without considerable variations in  $F_V$  or WSG (Poorter  
156 et al., 2010, Zanne et al., 2010). Similarly, for a constant fiber fraction ( $F_F$ ), trees can modulate WSG by  
157 increasing fiber wall thickness ( $F_{WT}$ ) (i.e., Zieminska et al., 2013). Hence, it appears that trees can adjust  $F_V$  or  
158  $K_S$  independently of WSG and mechanical stability (Hietz et al., 2016). It remains unclear, however, if these  
159 orthogonal relationships between  $F_V$ ,  $K_S$  and WSG are radially constant

160

161           In this study, we quantified radial changes in wood functional traits, and analyzed correlations between  
162 these traits, in 19 tree species from a lowland humid forest in Eastern Amazonia. Our general aim was to broaden  
163 our understanding of the anatomical bases of radial trends in wood specific gravity. In particular, we wanted to  
164 answer the following questions: (i) How does wood specific gravity change with tree diameter (ii) What are the  
165 main anatomical drivers of radial trends in wood specific gravity? (iii) Do vessel fraction and specific hydraulic  
166 conductivity vary independently of wood specific gravity as trees grow larger?

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## 174 MATERIALS AND METHODS

175

176 **Study site** — The research took place in the Paracou field station, a lowland tropical humid forest located in  
177 northern French Guiana (5° 18' N, 52° 55' W). The site has a mean annual temperature of 28.4°C, and annual  
178 rainfall averages 3.000 mm with a marked dry season from August to November, and a distinct rainy season  
179 between March and June (Wagner et al., 2011). In terms of floristic composition and species richness, the forest  
180 of Paracou is representative for northeaster Amazonia (ter Steege et al., 2006) and the Guiana Shield (ter Steege  
181 et al., 2000). Detailed descriptions of soils of Paracou can be found in Ferry et al., (2010) and Vincent et al.,  
182 (2011).

183

184 **Species and sampling** — At Paracou, a 25-ha and three 6.25-ha permanent plots were established, between  
185 1991 and 1992, to study the dynamics of an undisturbed tropical rain forest, and censuses of all stems with  
186 DBH > 10 cm have been conducted every five years since then (Gourlet-Fleury et al., 2004). Based on 23-year  
187 census data from these plots, we selected 19 tree species with broad gradients of variation in growth rates and  
188 shade-tolerance, and belong to some of the most dominant families at the site, namely Fabaceae, Lecythydaceae  
189 and Chrysobalanaceae (Table 1, Hérault et al., 2011, Baraloto *et al.*, 2012). Our study species also spanned a  
190 wide spectrum of mean wood specific gravity ranging from 0.30 to 0.97 (Table 2). In total, we sampled 65  
191 mature trees (DBH > 10 cm), with two to five individuals per species (Table 1). All wood samples were collected  
192 in Paracou, except for *Cordia alliodora*, *Schefflera morototoni*, *Cecropia obtusa* and *Miconia tschudyoides*,  
193 that were collected in a nearby secondary forest. Samples of eight species (e.g., all legume species, *Cordia*  
194 *alliodora* and *Bagassa guianensis*) were from previous studies (Bossu, 2015, Lehnebach et al., 2019).

195

196 Wood samples were collected, in 2014 and 2018, from stem discs taken at breast height, from cut-  
197 down trees. From each wood sample, wood segments of 2 x 2 cm size were cut and split every 0.5 cm from pith  
198 to bark. Whenever possible, heartwood and sapwood were distinguished based on color differences, and  
199 sapwood and heartwood lengths were measured. For each wood segment, we measured the radial position with  
200 respect to the pith, fresh volume and dry mass. Fresh volume was measured with the water displacement  
201 method, and dry mass was obtained after drying the segments at 103°C to a constant mass, for 24-72 h. WSG



202 per segment was defined as dry mass over fresh volume (Kollman and Coté 1968). For each tree, wood  
 203 anatomical analyses were conducted on the segments closest to the pith, and every 1.5 cm until reaching the  
 204 bark. To characterize wood anatomy, the cross-sectional surface of each wood segment was sanded using a  
 205 polishing machine with 1200-grit diamond discs, and then samples were cut with a GLS-1 sledge microtome  
 206 (Gärtner et al., 2015) to get a plane surface. Then, photographs were taken at 5-10 x objective lenses using a  
 207 reflected light (episcopic) microscope (BFMX, Olympus, Tokyo, Japan), equipped with a digital camera (Canon  
 208 EOS T6i; Canon Inc., Tokyo, Japan). For each wood segment, between 10-20 partially focused images were  
 209 taken and were then combined using Helicon Focus (Helicon Focus Ltd., Kharkov, Ukraine). Because of its  
 210 very high WSG (0.97), it was not possible to obtain high-quality anatomical images of *Bocoa prouacensis* and  
 211 this species was excluded from the anatomical analyses.

212

213 From each anatomical image (see Fig. S1), fractions of fibers ( $F_F$ ), vessels (i.e., vessel lumen,  $F_V$ ),  
 214 axial parenchyma ( $F_{AP}$ ), radial parenchyma ( $F_{RP}$ ) and total parenchyma ( $F_{TP}$ :  $F_{AP} + F_{RP}$ ) per cross-section were  
 215 measured in the whole image. To calculate cell fractions, wood cell types were manually colored using  
 216 Photoshop (Adobe Systems Incorporated, USA) and then added automatically using the batch function in the  
 217 software ImageJ (<https://imagej.nih.gov/ij/>). Moreover, in each anatomical image, three metrics related to  
 218 xylem vascular strategies were measured: Vessel lumen area ( $V_A$ ,  $\text{mm}^2$ ), vessel number ( $V_N$ , number of vessels  
 219 per  $\text{mm}^2$ ) and specific hydraulic conductivity ( $K_S$ ,  $\text{kg m MPa}^{-1} \text{s}^{-1} \text{h}$ ). To calculate  $V_A$  and  $V_N$ , all conduits within  
 220 each anatomical image were manually coloured, counted and measured.  $K_S$  was estimated according to the  
 221 Hagen-Poiseuille equation as

222

$$223 \quad K_S = \rho w / (128 \eta) V_D Dh^4 10^6$$

224

225 where  $\rho w$  is the density of water at 20° C ( $998.2 \text{ kg m}^{-3}$ ) and  $\eta$  is the viscosity of water at 20° C ( $1.002 \times 10^{-3}$   
 226  $\text{MPa s}$ );  $Dh$  is the mean hydraulically weighted vessel diameter given by

227

$$228 \quad Dh = (\sum D^4 / n)^{1/4}$$

229

230 where  $D$  is the average of the major and minor axis for each vessel cross-section (in mm) and  $n$  is the total  
231 number vessels (Tyree and Zimmermann 2002, Hietz et al., 2016). Fiber wall thickness ( $F_{WT}$ ,  $\mu\text{m}$ ) was measured  
232 by taking photographs with a 100x objective lens using a laser microscope (VK 9710, Keyence). Each cross-  
233 sectional image (see Fig. S2) was divided in four equal sections and 8 pairs of fibers were randomly selected in  
234 each section, for a total of 32 pairs of fibers per image. To obtain  $F_{WT}$ , double wall thickness was measured and  
235 then divided by two, using ImageJ.

236

237 **Data analyses**— To analyze radial gradients in WSG (question 1), we fitted separate linear models (LM) per  
238 species predicting WSG based on radial distance. We also evaluated non-linear equations in these LM, as  
239 curvilinear gradients in WSG are common among tropical trees (e.g., Williamson and Wiemann 2010a,  
240 Osazuwa-Peters et al., 2014). Previous studies examining non-linear radial trends in WSG have considered  
241 mainly quadratic equations (e.g., Osazuwa-Peters et al., 2014) which, although widely used and flexible, cannot  
242 describe some patterns commonly observed during tree growth. Therefore, we fitted linear or curvilinear  
243 functions (i.e., quadratic, logistic and cubic) to each WSG-radial distance species plot and compared these  
244 models based on Akaike's Information Criterion corrected for small sample sizes ( $AIC_C$ ), with lower  $AIC_C$   
245 scores indicating a better fit to the data. When the difference in  $AIC_C$  scores between two models was  $\leq 2$ , we  
246 selected the simpler model with fewer parameters (Burnham and Anderson 2002). Finally, we examined  
247 residual plots to confirm linear or non-linear trends. We also analyzed radial trends in wood anatomical traits  
248 for each species (see Table S1), we used linear or generalized linear models (GLM) to predict each anatomical  
249 trait based on radial distance. Yet, in these models we were not able to reliably test non-linear terms because  
250 for several trees, particularly the small-to-medium-sized ones, we had only a few radial anatomical  
251 measurements.

252

253 After examining radial trends in WSG, we studied the anatomical drivers of those trends (question 2).  
254 To do so, we analyzed a subset of our dataset consisting of 13 (excluding *B. prouacensis*) species that had  
255 significant radial trends in WSG (Table 3). First, we fitted linear mixed models with all possible predictors (i.e.,  
256 anatomical traits) and species and individuals as random factors. The best-fit model based was selected based

257 on AIC<sub>C</sub>, which penalizes models with additional parameters (Burnham and Anderson 2002), and it was as  
 258 follows:

259

260  $WSG \sim F_F + F_{WT} + F_{AP} + F_{RP} + (1 | \text{Species Individuals})$

261

262 We then fitted separate multiple regression models for each of the 13 species, predicting radial shifts in WSG  
 263 based on  $F_F$ ,  $F_{WT}$ ,  $F_{AP}$  and  $F_{RP}$ .  $F_{AP}$  was log-transformed to meet normality assumptions.

264

265 As  $F_V$  and  $K_S$  may vary independently from WSG across species (Zanne et al., 2010, Hietz et al., 2016),  
 266 we tested if this assumption still holds radially within trees (question 3). To do this, we fitted separate LM per  
 267 species predicting these traits (i.e.,  $F_V$  and  $K_S$ ) based on radial distance. In these models, we included a radial  
 268 distance-WSG interaction term ( $D \times WSG$ ). Both  $F_V$  and  $K_S$  were  $\log_{10}$  transformed to meet regression  
 269 assumptions. Lack of significance of the  $D \times WSG$  interaction term, accompanied by a significant radial change  
 270 in  $F_V$  or  $K_S$ , would mean that the radial trend of a given hydraulic trait was independent of WSG. All LM, GLM  
 271 and multiple regression models were fitted using the “MASS” package (Venables & Ripley 2002) in the  
 272 software R 3.6.1 (R Development Core Team 2019)

273

274

## 275 **RESULTS**

276

277 Overall, there was substantial variation in mean wood trait values across species (Table 2). Mean WSG ranged  
 278 from 0.30 in *S. morotoni* to 0.97 in *B. prouacensis* (2.9-fold variation, Table 2). Fibers, the most abundant  
 279 cell type, occupied on average 63.3% of wood cross-section and had the lowest variation between traits (1.83-  
 280 fold variation). Fiber wall thickness averaged 4.15  $\mu\text{m}$  and varied 4.34-fold between species. Total parenchyma  
 281 (axial + radial) was the second most abundant cell type with a mean fraction of 27.6% and a 3.5-fold variation.  
 282 Vessel fraction averaged at 8.94% (with 4.9-fold variation). Mean  $K_S$  varied from 46.9 to 330.1 ( $\text{kg m MPa}^{-1} \text{s}^{-1}$ )  
 283 with 7.17-fold variation (Table 2).

284

285 **Radial gradients in WSG and wood anatomical traits**—We found significant radial changes in WSG in 14 out  
 286 of the 19 study species (74%; Fig. 1, Table 3). Among them, positive gradients in WSG were observed in nine  
 287 species, mostly corresponding to fast-growing species (e.g., *C. obtusa*, *S. morototoni*) or semi shade-tolerants  
 288 (sensu Favrichon 1994; *Dicorynia guianensis* or *Eperua falcata*); while negative gradients were present in five  
 289 species (e.g., *B. prouacensis* or *Swartzia panacoco*; three of them are shade-tolerants). Radial gradients in WSG  
 290 were best fitted by linear models in eight species (57.1%), while quadratic and cubic models best explained  
 291 radial gradients in WSG in four (28.5%) and two (14.2%) species, respectively (Fig. 1, Table 3). The  
 292 coefficients of determination of these models (Table 3) suggest that radial trends in WSG are not only common  
 293 in the study site, but also substantial. Five species had no significant radial shifts in WSG. Not all species  
 294 showed significant trends in wood anatomical traits, and the signs and coefficient of determination of these  
 295 trends, when significant, usually varied between species. In general,  $F_F$ ,  $F_{AP}$  and  $F_{TP}$  tended to increase with  
 296 increasing radial distance (Fig. 2, Table S1).

297

298 **Anatomical drivers of radial gradients in WSG**—For the 13 species that had significant radial changes in WSG  
 299 (Table 3), we examined the anatomical traits underlying those trends by fitting multiple regression models.  
 300 These models predicted radial changes in WSG in only six species. Among these six species, radial variations  
 301 in WSG were predicted by different combinations of fiber and parenchyma traits (Table 4). There were two  
 302 main ways in which trees modulated fiber fractions and morphologies in order to increase WSG radially:  
 303 increasing fiber wall thickness ( $F_{WT}$ ) (e.g., *Bagassa guianensis* or *Shefflera morototoni*), or increasing both  $F_{WT}$   
 304 and fiber fraction ( $F_F$ ) (e.g., *Virola michelii* or *Miconia tschudyoides*).  $F_{AP}$  and  $F_{RP}$  had either positive or  
 305 negative effects on positive radial trends in WSG (Table 4).

306

307 **Links between vessel related traits and WSG**— Vessel fraction ( $F_V$ ) changed significantly from pith to bark in  
 308 nine species (Table 5). Of these species, the radial distance-WSG interaction term ( $DxWSG$ ) was significant in  
 309 only one species, indicating that these radial changes in  $F_V$  were largely independent from WSG (Table 5, Fig.  
 310 3). Specific hydraulic conductivity ( $K_S$ ) increased significantly with stem diameter in ten species (Table 5). In  
 311 three of these species, the  $DxWSG$  interaction term was significant, which indicates that variations in  $K_S$  were  
 312 in general independent of shifts in WSG.

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318 **DISCUSSION**

319

320 *Positive radial gradients in WSG and their anatomical drivers*— Similar to previous research (i.e., Hietz *et*  
321 *al.*, 2013, Plourde *et al.*, 2015), we found significant and positive radial gradients in WSG in all pioneer and  
322 semi shade-tolerant species (Fig.1, Table 3). A number of studies have suggested that radial gradients in WSG  
323 in fast-growing species reflect their growth and allocation strategy (i.e., Woodcock and Shier 2002, Hietz *et al.*,  
324 2013, Plourde *et al.*, 2015). For instance, juveniles of fast-growing species tend to produce low specific gravity  
325 (SG) wood to favor high growth rates; and later, when they reach more favorable canopy layers, they produce  
326 high SG wood, probably to enable crown expansion and to increase mechanical stability (Woodcock and Shier  
327 2002, Nock *et al.*, 2009, Osazuwa-Peters *et al.*, 2014). Then, positive radial gradients in WSG have been  
328 interpreted as providing mechanical advantage, since trees with high SG wood in the outer part of the trunk can  
329 achieve needed strength, at a lower construction cost, than trees with high SG in inner wood (Hietz *et al.*, 2013,  
330 Schüller *et al.*, 2013, Bossu *et al.*, 2018).

331

332 In contrast, our knowledge on the radial changes in wood anatomy underlying this growth strategy is  
333 still limited (Rungwattana and Hietz 2017). Zieminska *et al.*, (2013, 2015) have shown that similar values of  
334 WSG, particularly intermediate ones (c. 0.50-0.80), might be the product of different combinations of wood  
335 anatomies. Likewise, we found that positive radial gradients in WSG were driven by different combinations of  
336 fiber and parenchyma traits (Table 4, Fig. 2). Previous studies on fast-growing species have found that radial  
337 increments in WSG can be explained either by increments in fiber fractions (McDonald *et al.*, 1995) or in fiber  
338 wall thickness (Rungwattana & Hietz *et al.*, 2017). Here, we extend these findings by showing that there are  
339 two alternative ways in which trees can adjust fibers in order to increase WSG radially: (i) by simultaneously  
340 increasing fiber fractions ( $F_F$ ) and fiber wall thickness ( $F_{WT}$ ) (i.e., *Virola michelii* or *Miconia tshudyoides*,

341 Table 4, Fig. 2), or (ii) by increasing  $F_{WT}$  (i.e., *Bagassa guianensis* or *Schefflera morototoni*, Table 4, Fig. 2).  
342 Fibers are the most abundant cell type and tend to have thicker walls compared to other wood cells (Zieminska  
343 et al., 2013), and thus are expected to contribute to a large extent to WSG variations (Jacobsen et al., 2007,  
344 Martínez-Cabrera et al., 2009). On the other hand, we found that axial parenchyma fractions ( $F_{AP}$ ) and fiber  
345 fractions ( $F_{RP}$ ) can have either positive or negative effects on radial changes in WSG (Table 4). However, their  
346 overall influence on radial WSG variations should be small, since both axial and parenchyma cells tend to have  
347 thin walls of low tissue densities (i.e., Fujiwara 1992). The fact that positive radial gradients in WSG were  
348 underpinned by different radial shifts in fiber and parenchyma traits suggests that species with similar shade-  
349 tolerance may differ in their stem allocation patterns and functioning. For instance, species that increase WSG  
350 radially by increasing  $F_{WT}$ , also tend to decrease  $F_F$  towards the bark (Table 4). This suggests that these species  
351 might achieve needed strength while leaving more wood volume available for vessels or parenchyma cells, in  
352 comparison to species that adjust WSG radially by increasing both  $F_F$  and  $F_{WT}$ .

353

354 While there is a growing consensus that positive radial gradients in WSG represent a benefit in terms  
355 mechanical stability (i.e., Hietz *et al.*, 2013, Schüller et al., 2016, Bossu et al., 2018), it is still less clear what  
356 are the potential disadvantages of this growth strategy. Larjavaara and Muller-Landau (2010) showed that low-  
357 WSG species can achieve greater strength than high WSG species, at a lower construction cost, by building  
358 thicker stems. Yet, they also hypothesized that, for the same strength, low-WSG species would have higher  
359 maintenance costs compared to high-WSG species, because stem respiration is thought to be proportional to  
360 stem surface area. This hypothesis would hold in general for our study species, given that low WSG species  
361 usually attain larger stem diameters compared to high-density species (Table 2). However, although this  
362 hypothesis has received considerable interest and is partially supported by recent experimental evidence (e.g.,  
363 Rodríguez-Calcerrada et al., 2019), it does not consider radial variations in WSG that are prevalent in several  
364 forest types. The occurrence of these radial trends in WSG suggests that stem construction costs may change  
365 as trees grow. Moreover, while stem maintenance costs may be proportional to stem surface area (Larjavaara  
366 and Muller-Landau 2010), it is likely that stem respiration will be more linked to the fraction of living  
367 parenchyma cells (Rodríguez-Calcerrada et al., 2019). We observed contrasting radial trends in total  
368 parenchyma fractions among our study species (Table S1, Fig. 2), indicating that species might also have

369 distinct radial changes in stem respiration. We suggest that future studies should explore both radial changes in  
370 stem construction and maintenance costs in order to better understand the ecological significance of radial WSG  
371 variations.

372

373 **Negative radial trends in WSG**— We found significant and negative radial trends in WSG in five species (*B.*  
374 *prouacensis*, *Recordoxylon speciosum*, *E. falcata*, *Hirtella glandulosa* and *Sextonia rubra*; Fig. 1, Table 3). In  
375 all of these species, heartwood was clearly distinguished on the basis of color difference. It has been suggested  
376 that the deposition of wood extractives in the inner stem, during heartwood formation, may explain the  
377 occurrence of negative radial trends in WSG (Hietz et al., 2013, Lehnebach et al., 2019). Wood extractives are  
378 secondary compounds involved in defense (Hillis 1987), that can affect WSG via increments in wood dry mass.  
379 For example, Lehnebach et al., (2019) showed that heartwood extractives changed the magnitude of radial  
380 trends in WSG in *R. speciosum*, and both the magnitude and direction of radial shifts in WSG in *B. prouacensis*  
381 and *E. falcata*. In the case of *E. falcata* and *R. speciosum*, our results showed that radial shifts of WSG were  
382 unrelated to anatomical traits (Table 3), which indicates that heartwood extractives would be the main drivers  
383 of those trends. Thus, the negative radial shifts in WSG observed in these species likely reflect defensive needs,  
384 rather than mechanical requirements. Yet, the contribution of wood extractives to WSG variations may change  
385 considerably among species depending on their concentration (i.e., % of wood dry mass) and radial distribution.  
386 For instance, in *S. rubra* and *B. prouacensis* extractives contents are only slightly higher in heartwood compared  
387 to sapwood (Rodrigues 2010, Amusant et al., 2014), suggesting that their contribution to radial changes in WSG  
388 are small.

389

390 For some species, especially shade-tolerants, we did not find any significant radial shift in WSG (Table  
391 3, Fig 1) nor in wood anatomical fractions (Table S1, Fig. 2). This is in agreement with prior studies showing  
392 that radial shifts in WSG are less common and pronounced in shade-tolerant than in pioneer species (i.e.,  
393 Plourde *et al.*, 2015). One possible explanation to this trend is that shade-tolerants have no, or modest, radial  
394 shifts in wood traits because they tend to have inherent low trait plasticity (Valladares et al., 2000, Popma et  
395 al., 2002, Rozendal et al., 2006). In our study, shade-tolerant species had negative (i.e., *B. prouacensis*) or no  
396 (e.g., *Lecythis persistens*) radial trends in WSG or wood anatomical traits. These stem characteristics may be

397 particularly common in the forests of the Guiana Shield that have lower rates of gap formation than other  
398 Amazonian forests (Molino and Sabatier 2001) and are typically dominated by shade-tolerant species (ter  
399 Steege et al., 2000, 2006). Alternatively, the fact that we did not observe significant radial changes in wood  
400 traits for some species might be due to our measurement strategy. Since we measured anatomical traits every  
401 1.5 cm from pith to bark, we may not be able to properly capture the radial anatomical variation, when present,  
402 in some trees with low or intermediate stem diameters. Moreover, for most species we sampled trees with stem  
403 diameters lower than the mean diameters that species attain at our study site (Table 1). Then, much remains to  
404 be known on the magnitude, and ecological implications, of radial variations in wood functional traits at our  
405 study site.

406

407

408 ***Radial variations in vascular strategies***— Our results show that, in general,  $F_v$  and  $K_s$  vary independently of  
409 WSG from pith to bark (Table 5). These findings add to growing evidence indicating that these traits would be  
410 decoupled across species (Zanne et al., 2010, Fortunel et al., 2013, Hietz et al., 2016), and also radially within  
411 trees from tropical dry forests (Rungwattana and Hietz 2017). These results may have distinct, but non-mutually  
412 exclusive explanations. First, in our study species, a direct trade-off between  $F_v$  and WSG is unlikely since  
413 vessel lumens occupied, on average, a relatively small fraction of stem cross-sectional area (range: 4.30-21.1,  
414 average: 8.94; Table 2). Second, at least in humid forests, trees can modulate their WSG and  $K_s$ , without  
415 significant increments in fiber and vessel fractions, by producing thicker fibers and wider vessels, respectively  
416 (Zieminska et al., 2013, Hietz et al., 2016). Since WSG is considered in general a good indicator of  
417 biomechanical properties (King et al., 2006, Anten and Shieving 2010), the orthogonal relationship of  $F_v$  and  
418  $K_s$  with WSG has been interpreted as evidence that hydraulic and mechanical functions are decoupled (Hietz  
419 et al., 2016). This independence between functions may have important implications for understanding resource  
420 allocation patterns in high-diversity forests (Marks and Lechowicz 2006, Li et al., 2015). If trees can modulate  
421 hydraulics independently from mechanics during their life-cycles, then different trait combinations and  
422 ecological strategies might be possible among coexisting species. For instance, species with similar means and  
423 ranges of  $F_v$  (roughly 5.77 and 2.72-11.3, respectively) may have either positive (e.g., *P. nitida*), negative (i.e.,  
424 *E. falcata*) or even absent radial trends in WSG (e.g., *Eschweilera sagotiana*).



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428

429 **CONCLUSIONS**

430

431 This study illustrates the contrasting radial variations in WSG and wood anatomical traits that occurs in several  
432 tree species from a humid tropical forest in Eastern Amazonia. Most of the species showed significant radial  
433 shifts in WSG and/or in wood anatomical traits. Our results indicate that positive radial gradients in WSG were  
434 mostly present in fast growing species and that these gradients were driven by different combinations of fiber  
435 and parenchyma traits. In contrast, negative radial trends in WSG were mostly present in shade-tolerant species,  
436 but were unrelated to radial changes in wood anatomy and appear to be more related, in some cases, to the  
437 accumulation of secondary compounds. Interestingly, some species, mostly shade-tolerants, did not exhibit  
438 significant radial changes in WSG nor in wood anatomical fractions. Previous studies at global and local scales  
439 have shown that, across species, WSG, vessel fraction and specific hydraulic conductivity vary independently  
440 from one another. Here we confirm that independence between these traits is in general maintained radially  
441 within stems.

442

443

444 Overall, our study provides valuable insights into radial variations in wood functional traits across  
445 tropical, humid forest tree species. These radial changes in wood traits are likely to be important to expand our  
446 knowledge of stem allocation patterns and tree life-history strategies. First, given that some wood traits can  
447 vary substantially from pith to bark, the study of wood trait variations across species or along environmental  
448 gradients would be improved by taking into account the effect of tree stem diameter. For instance, the common  
449 assumption that community WSG decreases with soil fertility or with mean annual precipitation may be  
450 partially explained by possible differences in stem diameters between sites. Second, radial changes in wood  
451 traits can be of central importance in explaining size-related variations in species demographic rates, that are  
452 frequent among different forest ecosystems. Lastly, as WSG is an important predictor of above-ground biomass

453 (AGB) estimations, considering radial trends in WSG may increase the accuracy of AGB estimations at both  
454 the tree and stand level.

455

456

457 **ACKNOWLEDGMENTS**

458

459 We are very grateful to Jonathan Prunier for laboratory and field support, and to Pascal Petronelli for his help  
460 with botanical identification. We kindly thank Soepe Koese for his help collecting and preparing the wood  
461 samples. We would also like to thank Camila Monje and Laura Baldion who assisted in processing anatomical  
462 images, and to Julie Bossu for providing some wood samples. The study was designed by A.G.M., J.M.P., B.C.  
463 and J.B. Most wood samples were collected by R.L. and A.G.M. Additional samples were provided by B.C.,  
464 J.B. and S.L. Anatomical images were processed by A.G.M. and K.R. Data analyses were performed by A.G.M.  
465 with contributions from J.M.P. The first draft of the manuscript was written by A.G.M. with inputs from J.M.P.  
466 All authors contributed equally to the writing and interpretation of advanced versions of the manuscript.

467

468 **FUNDING**

469

470 This study was funded by a student grant awarded to A.G.M by COLCIENCIAS (Colombian Agency for  
471 Science and Technology. Grant 476), and a field grant from the University of Guyane in the framework of the  
472 Erasmus+ Program. We know of no conflicts of interest associated to this manuscript.

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791 **TABLES**

792 **Table 1.** Study species, family, number of trees sampled (n), mean diameter at breast height of trees sampled (DBH<sub>S</sub>), mean and maximum diameter at breast  
 793 height of each species (DBH<sub>M</sub> and DBH<sub>MAX</sub>, respectively), ecological guilds according to Favrichon (1994), relative growth rates (RGR, mm.mm<sup>-1</sup> y<sup>-1</sup>), and leaf  
 794 habit; for 19 tree species from Eastern Amazonia. DBH<sub>M</sub> and DBH<sub>MAX</sub> were calculated based on data from one 25-ha and three 6.25-ha permanent plots  
 795 established in Paracou (see Materials and methods). DBH<sub>M</sub> of *C. alliodora* were obtained from Bossu (2015), while DBH<sub>MAX</sub> were obtained from Vega (1977).  
 796 DBH<sub>MAX</sub> for each species was estimated averaging values of the five largest individuals. RGR were calculated based on 20-year census data from permanent plots  
 797 established in Paracou.

Species	Family	n	DBH <sub>S</sub> (cm)	DBH <sub>M</sub> (cm)	DBH <sub>MAX</sub> (cm)	Ecological guild	RGR	Leaf habit
<i>Bagassa guianensis</i>	Moraceae	5	25.1	35.8	105.7	Long-lived pioneer-Canopy		Deciduous (Loubry, 1994)
<i>Bocoa prouacensis</i>	Fabaceae	3	12.3	28.6	52.7	Shade-tolerant-Understory	3.81	Evergreen (Levionnois et al., 2020)
<i>Cecropia obtusa</i>	Urticaceae	3	23.1	15.7	33.3	Pioneer-Understory	5.30	
<i>Cordia alliodora</i>	Boraginaceae	3	44.4	38.9	85.2	Long-lived pioneer-Canopy		Deciduous (Loubry, 1994)
<i>Dicorynia guianensis</i>	Fabaceae	5	22.2	47.3	94.7	Semi shade-tolerant-Canopy	2.76	Deciduous (Loubry, 1994)
<i>Eperua falcata</i>	Fabaceae	5	45.5	47.7	71.8	Semi shade-tolerant-Canopy	1.91	Deciduous (Loubry, 1994)
<i>Eschweilera coriacea</i>	Lecythidaceae	2	30.3	38.2	63.3	Shade-tolerant-Canopy	1.55	Evergreen (Levionnois et al., 2020)
<i>Eschweilera sagotiana</i>	Lecythidaceae	3	20.8	41.4	69.2	Shade-tolerant-Canopy	1.41	Evergreen (Levionnois et al., 2020)
<i>Hirtella glandulosa</i>	Chrysobalanaceae	2	30.3	17.1	40.3	Shade-tolerant-Understory	1.78	Evergreen (Carneiro et al., 2021)
<i>Lecythis persistens</i>	Lecythidaceae	5	22.3	35.9	65.8	Shade-tolerant-Understory	0.91	Evergreen (Levionnois et al., 2020)
<i>Licania alba</i>	Chrysobalanaceae	5	23.7	28.8	49.3	Shade-tolerant-Canopy	0.82	Evergreen (Levionnois et al., 2020)
<i>Miconia tschudyoides</i>	Melastomataceae	2	21.2	15.7	25.8	Pioneer-Understory	1.90	
<i>Oxandra asbeckii</i>	Annonaceae	2	24.6	19.5	33.3	Shade-tolerant-Understory	0.72	
<i>Parkia nitida</i>	Fabaceae	5	23.5	63.1	101.3	Pioneer-Canopy	6.98	Deciduous (Loubry 1994)
<i>Recordoxylon speciosum</i>	Fabaceae	3	14.3	38.2	64.4	Semi shade-tolerant-Canopy	2.18	Deciduous (Loubry 1994)
<i>Schefflera morototoni</i>	Araliaceae	3	41.2	38.6	49.3	Pioneer-Canopy	4.3	Deciduous (Loubry, 1994)
<i>Sextonia rubra</i>	Lauraceae	3	42.4	50.5	100.2	Semi shade-tolerant-Canopy	2.15	Deciduous (van der Werff, 1997)
<i>Swartzia panacoco</i>	Fabaceae	3	20.5	25.4	51.3	Shade-tolerant-Canopy	0.76	Deciduous (Loubry, 1994)
<i>Virola michelii</i>	Myristicaceae	3	31.5	31.8	64.5	Pioneer-Canopy	2.37	Deciduous (Loubry, 1994)

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799 **Table 2.** Summary characteristics of wood traits measured on 18 tree species from a lowland tropical forest in  
 800 Eastern Amazonia. Mean, standard deviation (SD), range and n-fold variation are shown.

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<b>Trait</b>	<b>Abb rev.</b>	<b>Unit</b>	<b>Mean</b>	<b>SD</b>	<b>Range</b>	<b>n-fold variation</b>
Wood specific gravity	WSG	unitless	0.61	0.07	0.30-0.97	2.9
Fiber fraction	F <sub>F</sub>	% area	63.3	6.89	42-77	1.83
Fiber wall thickness	F <sub>WT</sub>	μm	4.15	1.29	1.72-7.47	4.34
Vessel fraction	F <sub>V</sub>	% area	8.94	2.96	4.30-21,2	4.9
Axial parenchyma fraction	F <sub>AP</sub>	% area	11.5	9.06	1.68-29.1	17.3
Radial parenchyma fraction	F <sub>RP</sub>	% area	15.8	3.69	6,09-27,7	4.54
Total parenchyma fraction	F <sub>TP</sub>	% area	27.6	5.33	12.6-44.2	3.5
Vessel lumen area	V <sub>A</sub>	mm <sup>2</sup>	0.015	0.006	0.01-0.03	3
Vessel number	V <sub>N</sub>	mm <sup>-2</sup>	5.68	4.12	0.87-21.1	26
Specific hydraulic conductivity	K <sub>S</sub>	kg m s <sup>-1</sup> MPa <sup>-1</sup> / mm <sup>2</sup>	147.7	18.1	46.9-330.1	7.17

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804 **Table 3.** Linear and non-linear models predicting WSG based on radial distance. Best fit model and its  
 805 parameters are shown for each species. Coefficient of determination ( $R^2$ ) of each model is provided.  
 806 Significance levels are: \*,  $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ . Significant radial trends ( $P < 0.05$ ) are given  
 807 in bold.

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Species	WSG	
	Best-fit model	$R^2$
<i>Bagassa guianensis</i>	Linear	<b>0.95</b> **
<i>Bocoa prouacensis</i>	Linear	<b>0.72</b> **
<i>Cecropia obtusa</i>	Cubic	<b>0.90</b> *
<i>Cordia alliodora</i>	Linear	<b>0.91</b> *
<i>Dicorynia guianensis</i>	Linear	<b>0.93</b> **
<i>Eperua falcata</i>	Quadratic	<b>0.69</b> **
<i>Eschweilera coriacea</i>	Linear	0.01
<i>Eschweilera sagotiana</i>	Linear	0.03
<i>Hirtella glandulosa</i>	Linear	<b>0.48</b> *
<i>Lecythis persistens</i>	Linear	0.02
<i>Licania alba</i>	Linear	0.35
<i>Miconia tschudyoides</i>	Linear	<b>0.71</b> ***
<i>Oxandra asbeckii</i>	Linear	0.08
<i>Parkia nitida</i>	Linear	<b>0.88</b> **
<i>Recordoxylon speciosum</i>	Quadratic	<b>0.87</b> *
<i>Schefflera morototoni</i>	Quadratic	<b>0.65</b> **
<i>Sextonia rubra</i>	Cubic	<b>0.46</b> **
<i>Swartzia panacoco</i>	Quadratic	<b>0.93</b> **
<i>Virola michelii</i>	Linear	<b>0.94</b> *



827 **Table 4.** Effects of wood anatomical fractions on radial variations of WSG variations for species ( $n = 13$ ) that  
828 had significant radial trends in WSG (see Table 3). Multiple  $R^2$  values of the corresponding multiple regression  
829 models, and t-values for each trait are shown. (+) or (-) gives the sign of the effects of wood anatomical traits  
830 on WSG variations. Significance levels are: \*,  $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\*,  $P < 0.001$ . Significant effects ( $P <$   
831  $0.05$ ) are given in bold.  
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Species	Wood anatomical fractions				
	$F_F$	$F_{WT}$	$F_{RP}$	$F_{AP}$	$R^2$
<i>Bagassa guianensis</i>	<b>2.41(-) *</b>	<b>3.56(+)**</b>	<b>1.69 (+) *</b>	0.59	0.77
<i>Cecropia obtusa</i>	0.21	0.24	0.51	0.46	0.45
<i>Cordia alliodora</i>	1.52	0.56	0.32	1.21	0.34
<i>Dicorynia guianensis</i>	0.65	0.21	0.03	1.14	0.64
<i>Eperua falcata</i>	0.31	0.41	0.98	1.04	0.53
<i>Hirtella glandulosa</i>	0.14	0.32	1.02	1,71	0.51
<i>Miconia tschudyoides</i>	<b>2.48(+)*</b>	<b>3.76(+)**</b>	<b>2.05(-)*</b>	0.87	0.79
<i>Parkia nitida</i>	<b>2.15(-)*</b>	0.06	1.25	<b>3.95(+)**</b>	0.72
<i>Recordoxylon speciosum</i>	1.12	0.03	0.72	1.46	0.62
<i>Schefflera morototoni</i>	<b>2.63(-)*</b>	<b>2.37(+)*</b>	1.42	<b>2.47(-)*</b>	0.92
<i>Sextonia rubra</i>	<b>2.41(-)*</b>	0.02	<b>2.31(+)*</b>	<b>3.22(-)**</b>	0.36
<i>Swartzia panacoco</i>	1.41	0.51	1.11	0.45	0.85
<i>Virola michelii</i>	<b>2.70(+)*</b>	<b>3.75(+)**</b>	0.72	<b>2.92(-)**</b>	0.82

834 Note: *B. prouacensis* was excluded from anatomical analyses, see Material and meth

835 **Table 5.** Linear models predicting vessel fraction ( $F_V$ ) and specific hydraulic conductivity ( $K_S$ ) based on radial  
836 distance (D), and effects of WSG on significant radial trends in  $F_V$  and  $K_S$ . (+) or (-) gives the sign of  $F_V$  and  
837  $K_S$  radial trends. Significance levels are: \*,  $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\*,  $P < 0.001$ . Significant radial trends ( $P <$   
838  $0.05$ ) in  $K_S$  and  $K_S$  are given in bold. Coefficient of determination ( $R^2$ ) for each model, and Chi-square statistic  
839 ( $X^2$ ) for each interaction term, are provided. Non-significant effects of the interaction term (DxWSG) indicate  
840 that radial shifts of  $F_V$  or  $K_S$  are unrelated to WSG.

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Species	$F_V$		$K_S$	
	D	DxWSG	D	DxWSG
	$R^2$	$X^2$	$R^2$	$X^2$
<i>Bagassa guianensis</i>	<b>0.62(+)</b> ***	<b>30.1</b> ***	<b>0.58(+)</b> ***	<b>1.29</b> ***
<i>Cecropia obtusa</i>	<b>0.47(+)</b> **	0.04	0.08(+)	3.21
<i>Cordia alliodora</i>	0.24	0.45	-0.02(-)	4.72
<i>Dicorynia guianensis</i>	0.14	0.71	<b>-0.09(+)</b> *	1.72
<i>Eperua falcata</i>	<b>0.14(-)</b> *	0.82	<b>0.30(+)</b> **	<b>4.24</b> *
<i>Eschweilera coriácea</i>	<b>0.47(+)</b> *	1.88	<b>0.69(-)</b> **	1.37
<i>Eschweilera sagotiana</i>	0.22	0.15	<b>0.94(+)</b> **	<b>12.6</b> *
<i>Hirtella glandulosa</i>	-0.04	0.05	-0.16(-)	0.87
<i>Lecythis persistens</i>	<b>0.08(+)</b> *	0.95	0.41(+)	0.14
<i>Licania alba</i>	0.10	1.43	<b>0.07(-)</b> **	3.21
<i>Miconia tschuyoides</i>	0.03	0.28	<b>0.56(-)</b> *	2.84
<i>Oxandra asbeckii</i>	<b>0.17(+)</b> *	1.12	<b>0.32(-)</b> *	1.37
<i>Parkia nitida</i>	0.32	0.11	-0.09(+)	0.98
<i>Recordoxylon speciosum</i>	0.04	0.17	0.04(-)	1.56
<i>Schefflera morototoni</i>	<b>0.51(+)</b> *	0.21	<b>0.30(+)</b> *	2.61
<i>Sextonia rubra</i>	<b>0.54(+)</b> **	0.38	<b>0.54(+)</b> **	2.71
<i>Swartzia panacoco</i>	-0.03	0.31	0.47(-)	5.21
<i>Virola michelii</i>	<b>0.15(-)</b> *	0.26	0.12(-)	1.07

842 FIGURES

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844 Fig. 1. Radial trends in WSG in 19 tree species from a lowland tropical forest in Eastern Amazonia. Grey and black dots represent individual

845 trees and species-mean values, respectively. Error bars denote standard deviation. Coefficients of determination ( $R^2$ ), significance levels (n.s.:

846  $P > 0.05$ ;  $P < 0.05$ ; \*\*:  $P < 0.01$ ; \*\*\*:  $P < 0.001$ ), and best-fit models (C, cubic; L, linear; and Q, quadratic) are provided (see Table 3).

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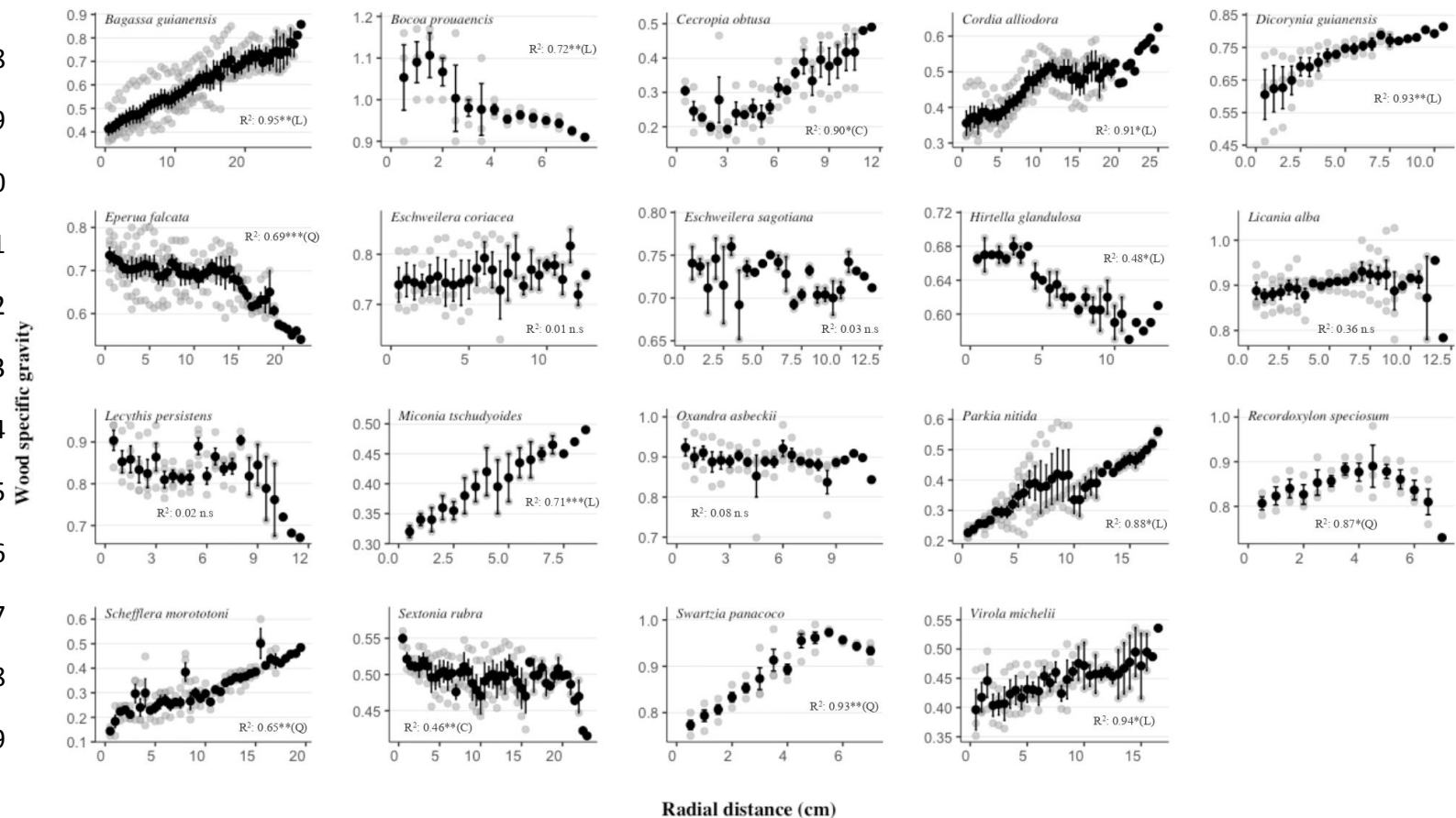
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860 **Fig. 2.** Radial variations in wood cell fractions and fiber wall thickness (black line;  $F_{WT}$ ) of 18 tree species from Eastern Amazonia.

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