

1 **Wood density variation across an Andes-to-Amazon elevational gradient**

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61 We declare that there are no conflicts of interest.

62

63 **Author contributions:**

64 William Farfan-Rios collected and analyzed the data and drafted the manuscript. Miles R.

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70 **Statement of inclusion:**

71 Our study brings together scientists from different countries, including authors from Peru, where
72 the study was carried out. Local authors were instrumental from the start of the study in
73 collecting the field data to editing the manuscript. We also work closely with the National
74 Service of Natural Areas Protected by the State (SERNAP-Manu), with whom we share our
75 results to contribute to managing the Manu National Park.

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78 **Data availability statement:**

79 The Andes Biodiversity and Ecosystem Research Group (ABERG) is a team of researchers
80 dedicated to understanding biodiversity, species distribution, and ecosystem function in the
81 Peruvian Andes. ABERG is committed to data exchange within the scientific community and
82 promoting collaboration among other tropical ecosystem scientists. For more information and to
83 request data, contact Miles Silman (<http://www.andesconservation.org/>). The ABERG wood
84 density dataset used in our study is deposited in the Zenodo digital repository
85 (<https://doi.org/10.5281/zenodo.10864740>). Global Wood Density Data Base was extracted from
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87 plots data was extracted from the ForestPlots database (<https://forestplots.net/>).

88

89 **Abstract**

90 **1.** Understanding how functional traits are related to species diversity and ecosystem properties
91 is a central goal of ecology. Wood density is a trait that integrates many aspects of plant form
92 and function and is highly variable among species. Previous studies of wood density across
93 elevational gradients have been based on limited sampling and have reported declines with
94 increasing elevation, though even this simple pattern remains unknown, much less its underlying
95 functional and evolutionary relationships.

96 **2.** Here, we use one of the longest and most speciose elevational gradients in the world,
97 extending from the Andean tree line to the Amazon basin, to test the extent to which elevation,
98 species composition, phylogenetic affinity, and forest structure determine variation in wood
99 density. Using field-collected wood samples and global databases, we assigned wood density to
100 1231 species and 31,330 stems across 41 (47.5 ha) mature forest plots arrayed across a 3,500 m
101 vertical gradient.

102 **3.** Our results show that mean wood density, either weighted by abundance, basal area, or
103 species, was highly variable but tended to decline from low to middle elevations and increase
104 again from mid-elevations to the tree line. As a result of this non-linearity, forests at the Andean
105 tree line had higher wood density than their lowland Amazon counterparts. We observed an
106 abrupt transition in wood density at the lower limit of persistent cloud formation (cloud base),
107 where the lowest wood density values were found. The decline of wood density is attributed to a
108 significant shift in life forms, with an abundance of tree ferns at middle elevations and a higher
109 probability of landslides and disturbances favoring a suite of traits associated with low wood
110 density, such as softer wood and higher elasticity. Species turnover explained most of the

111 among-species variation across the gradient, with elevation having no consistent effect on
112 within-species variation in wood density.

113 **4.** Together, both gradual compositional changes and sharp local changes in the importance of
114 non-dicot life forms, such as arborescent ferns and palms, define patterns of forest-level carbon
115 density, with wood density *per se* controlling ecosystem properties across the Andes-to-Amazon
116 elevational gradient.

117

118 **Keywords:** Amazon, Andes, elevational gradient, functional trait, species composition, wood
119 density

120 **Introduction**

121 Understanding how functional traits are related to species diversity and ecosystem
122 properties is a central goal of ecology, and it is also important to understand ecosystem services,
123 biodiversity conservation, and ecosystem responses to global change (Asner *et al.*, 2016; Neyret
124 *et al.*, 2016; Fyllas *et al.*, 2017). Climate and landscape gradients are efficient natural
125 laboratories for investigating the environmental controls on ecosystem function and diversity
126 (von Humboldt, 1838; Malhi *et al.*, 2010). Among natural gradients, the Amazon-Andes region
127 is among the longest environmental gradients and contains the most diverse and complex forests
128 globally (Gentry, 1995; Silman, 2014). In this study, we focus on the basic wood-specific gravity
129 (hereafter wood density) as an integrating functional trait of the ecosystem that can capture the
130 influence of environmental variables (e.g., temperature and moisture), forest architecture, and
131 mechanical characteristics along elevational gradients (Sperry, Meinzer and McCulloh, 2008;
132 Chave *et al.*, 2009). Understanding variations in wood density can give insights into tree life
133 history strategies, growth rate, and the role of climate and disturbance in tree demography (Putz
134 *et al.*, 1983; Swenson and Enquist, 2007; Poorter *et al.*, 2008; Adler *et al.*, 2014).

135

136 *Inter- and intraspecific wood density variability*

137 Wood density is a functional trait that varies between species, within species, and within
138 individual ecological functions. Inter- and intraspecific variation in wood density is closely
139 related to diameter growth rate (Putz *et al.*, 1983; Muller-Landau, 2004; King *et al.*, 2005),
140 hydraulic properties of the plant (Zanne *et al.*, 2010), and other wood properties such as porosity,
141 resistance, and the number of vessel cells (Chave *et al.*, 2009; Fortunel *et al.*, 2014). At the
142 community level, variation in wood density is often related to forest successional stage and life

143 history trade-offs between light-demanding and shade-tolerant species. Fast-growing and light-
144 demanding species typically have lower wood density values than shade-tolerant species (Chave
145 *et al.*, 2009), though the variability in the relationship between the rate of growth and wood
146 density is high and subject to multidimensional trade-offs (Rüger *et al.*, 2012) with some fast-
147 growing species have the highest wood density values recorded in tropical forests (e.g., *Tabebuia*
148 spp.). The importance of within-species variation in wood density vs. among-species variation is
149 critical to understanding the community-level importance of wood density and its implication in
150 ecosystem functioning. Even less understood are the differences in wood density among life
151 forms, e.g., true trees vs. arborescent life forms without secondary xylem (e.g., palms and tree
152 ferns). Varying abundances of these life forms are likely to affect ecosystem-level attributes such
153 as carbon storage.

154

155 *Wood density variation across tropical environmental gradients*

156 Existing studies of tropical forests across geographic and environmental gradients suggest
157 high variation in wood density within and among tree communities (Williamson, 1984; Fortunel
158 *et al.*, 2014). For example, across the Amazon basin, wood density is higher in the central and
159 eastern Amazon than in northwestern Amazonia, both at the species level (Muller-Landau, 2004;
160 Chave *et al.*, 2006) and stand level per stem basis (Baker *et al.*, 2004). This pattern can be
161 explained by the disproportionate abundance and diversity of taxa with high wood density values
162 associated with poor soils found in central and eastern Amazonia (Baker *et al.*, 2004; Muller-
163 Landau, 2004; ter Steege *et al.*, 2006). However, there is still uncertainty about whether these
164 patterns are caused by changes in wood density within all species in a community or, as tree
165 communities comprise a few abundant species and many rare species (Pitman, Silman and

166 Terborgh, 2013; ter Steege *et al.*, 2013). Patterns may be driven by hyperdominants or
167 oligarchs—species that combine high local density with broad distributional ranges in Amazonia.

168 Of all the gradients in the Neotropics, the forested gradient from the tropical high Andes
169 to Amazonian lowlands has the largest functional diversity and species richness and is likely the
170 highest-richness and plant functional diversity gradient on Earth (Asner *et al.*, 2016). Though
171 wood density is a key functional trait that links plant diversity with ecosystem function in
172 tropical forests, our knowledge of this trait along environmental gradients in the Neotropics is
173 incomplete, measured only at the lower end (0–2500 m) of an elevation gradient extending up to
174 4000 m, and only at the species level (Chave *et al.*, 2006). This leads to important questions. (1)
175 Given that leaf canopy traits are highly variable along elevational gradients (Asner *et al.*, 2016;
176 Neyret *et al.*, 2016), what is the pattern of wood density variation? (2) How is wood density
177 related to elevation *per se*, as indicated by within-species variation based on environmental
178 changes vs. turnover in species—and even deeper phylogenetic conservatism?

179 We investigated the variation of wood density as a functional trait in an elevational
180 gradient spanning ~3500 m from the Andean tree line to the Amazon basin on the eastern slope
181 of the Peruvian Andes. To our knowledge, this is the first study in the Neotropics that assesses
182 changes in wood density on an extensive elevational gradient using both field-collected wood
183 samples and plot-based sampling approaches, including trees, palms, and tree ferns. We ask (1)
184 what is the pattern of intra- and inter-specific variation in wood density across the Andes-to-
185 Amazon gradient?; (2) What is the effect of elevation on community wood density variation and
186 distribution, and how does this pattern differ when communities are defined by species
187 composition and stem abundance?; (3) What is the relationship between wood density and stem
188 size across the elevation gradient?

189

190 **Methods**

191 *Study site and climate*

192 The study was performed on the eastern slope of the Peruvian Andes along an elevational
193 gradient extending from the Andean tree line at 3700 m to the Amazon basin at 190 m in the
194 Manu Biosphere Reserve (11.8564° S, 71.7214° W) and Tambopata National Reserve (12.9206°
195 S, 69.2819° W). Mean annual temperature decreases linearly along the gradient with increasing
196 elevation at a lapse rate of 5.2 °C/km, ranging from ~27 °C at the lowest elevations to ~6 °C at
197 the tree line (Rapp and Silman, 2012; Malhi *et al.*, 2016). Mean annual precipitation varies
198 across the gradient from 2448 to 5500 mm yr⁻¹, with significant inter-annual variability (Rapp
199 and Silman, 2012; Malhi *et al.*, 2016). There also is distinct seasonality in rainfall, with the
200 highest rainfall in January and February and the lowest in June and July. Winds vary little
201 throughout the year, with the dominant pattern being upslope winds during the day and
202 downslope winds at night (Rapp and Silman, 2012). The study area has high cloud frequency in
203 contrast to many other areas of the eastern slope of the Andes, with clouds present in all seasons.
204 Along the elevational gradient, the cloud base zone is estimated to be between 1500–2000 m,
205 with the highest mean annual cloud frequency between 2000–3500 m (Halladay, Malhi and New,
206 2012).

207

208 *Wood density calculation*

209 We focused sampling on the dominant montane forest species because they are poorly or
210 unrepresented in global databases. In our study area, we have registered 908 arborescent species
211 above 1000 m elevation, and our field-taken wood samples comprise 34% of those species. We

212 collected wood cores from 892 individuals representing 311 species of the dominant arborescent
213 life forms—including trees, tree ferns (hereafter ferns), and palms from 2009 to 2015. We
214 stratified sampling of wood cores across the gradient to ensure coverage of a broad range of taxa
215 and to collect at least one individual for every species at each elevation. Core samples were
216 collected in 51 sites ranging from 346 to 3650 m of elevation (Fig. 1). An increment borer was
217 used to extract wood core samples for trees and palms ≥ 10 cm diameter at breast height (DBH).
218 The DBH of the sampled individuals ranged from 10 to 85 cm, and core samples were extracted
219 from 1 to 1.3 m above the ground. For trees and palms, the wood cores were taken from the
220 heartwood to the bark to capture density variation within the trunk. For arborescent ferns, sliced
221 samples were taken from the trunk-like rhizomes in six different sections, and the average
222 density value of the individual was used. Core samples were taken from individuals of targeted
223 species outside of the permanent plots across the gradient (see below “inventory plot data”
224 section) to avoid effects on plants that are part of long-term studies.

225 All values here are reported as a *wood basic specific gravity*, which is defined as oven-
226 dry mass divided by its green volume (Fearnside, 1997; Chave *et al.*, 2006; Williamson and
227 Wiemann, 2010) and henceforth called *wood density* in the text for simplicity. Wood density was
228 calculated using the water displacement method with all samples oven-dried to constant mass
229 and weighted to the nearest 0.001 g (Chave *et al.*, 2006). Values of wood density were first
230 calculated at oven-dry temperature at ~ 80 °C. Because of the possible presence of bond water in
231 the wood samples (Williamson and Wiemann, 2010), we used a sub-sample ($n = 145$) to
232 calculate wood density at 105 °C. We developed a correction equation (105 °C WD = $- 0.0113 +$
233 0.9969×80 °C WD; Fig. S1) that was applied to calibrate the wood density values of the rest of
234 the wood samples. We observed no significant difference among the wood density values at 105

235 °C and 80 °C (Mann-Whitney-Wilcoxon test, $n = 145$, $p = 0.31$). The overall mean difference
236 between wood density values at 105 °C and 80 °C was $2.4 \% \pm 0.38$ (95 % CI).

237

238 *Inventory plot data*

239 Plot data were collected from 41 (47.5 ha) permanent mature forest plots across an
240 elevation gradient ranging from 190 to 3625 m elevation, extending from lowlands through the
241 montane forest up to the Andean tree line. A network of 24 1-ha permanent plots was established
242 and monitored by the Andes Biodiversity and Ecosystem Research Group—ABERG ranging
243 from 387 to 3625 m elevation (ABERG PlotData, 2020). Additionally, 17 (23.5 ha) permanent
244 plots were established by various investigators in lowland forests and are now monitored by the
245 Amazon Forest Inventory Network—RAINFOR (Fig. 1). The RAINFOR plot data were
246 extracted from the ForestPlots.net database (Lopez-Gonzalez *et al.*, 2011). The permanent forest
247 plots contain 31,330 stems greater than 10 cm DBH and encompass 1,950 species (of which 35%
248 are morphospecies). Overall, the registered species in the transect belonged to 408 genera and
249 111 families (*sensu* APG IV).

250

251 *Botanical identification*

252 All botanical vouchers taken with the wood core collections were identified and then
253 compared and standardized with the permanent forest plots vouchers that were deposited in the
254 Peruvian and USA herbaria (CUZ, HUT, MOL, USM, and DAV, MO, F, and WFU,
255 respectively). Additionally, local flora and plant checklists were used as references (Pennington,
256 Reynel and Daza, 2004; Farfan-Rios *et al.*, 2015; Vasquez M. and Rojas G., 2016), and plant
257 identifications were also confirmed by taxonomic experts. The APG IV classification (Chase *et*

258 *al.*, 2016) was followed for the taxonomy names, and the Taxonomic Name Resolution Service
259 (TRNS) online application was used to standardize scientific plant names (Boyle *et al.*, 2013).

260

261 *Data analysis*

262 We analyzed wood density interspecific variation against elevation using each individual
263 of a given species sampled in the field. A restricted maximum likelihood (REML) analysis was
264 used to test the inter-specific variance of wood density across phylogenetic levels along the
265 gradient (Messier, McGill and Lechowicz, 2010). Variance partitioning analysis was done using
266 the *lme* and *varcomp* functions in R where a generalized linear model was fitted to the variance
267 across four scales nested levels: *species*, *genus*, *family*, and *plot*. Variance partitioning allowed
268 us to test the role of phylogeny and plot-to-plot variability including elevation. To test the effect
269 of elevation on intra-specific variation in wood density, we used a subset of the field-collected
270 samples. We used 46 species with ≥ 5 individuals that were present at least in two research sites
271 along the gradient. We then calculated the slopes of the linear regression models for each of the
272 selected species to observe the distribution of slopes and assess the positive, negative, or non-
273 relationship with elevation.

274 To analyze wood density variation across the elevational gradient at the plot level, we
275 calculated an average species wood density value derived from the wood samples collected in the
276 field (311 species, 892 individuals), and those values were assigned to each stem of a given
277 species in the plot network across the transect. For stems with no measured density values from
278 the transect, we incorporated wood density values from the Global Wood Density Data Base
279 (Zanne *et al.*, 2009). Overall, we compiled 1,231 forest taxa from field-collected samples and
280 published resources (Table S1). When density values were unavailable from the combined

281 datasets of field-published resources at the species level, the mean values at the genus or family
282 level were used. This was the case for the unidentified individuals to a species level
283 (morphospecies) that accounted for 13% of the total individuals. The local plot-level mean value
284 was used for the unknown taxa (0.8% of all taxa). We then calculated the mean wood density of
285 each plot in two ways. First, we calculated the average wood density across all species present
286 in each plot (species mean WD), and then we calculated the mean wood density by weighting
287 each species by its number of stems (stem-weighted WD). In addition, species mean WD was
288 also weighed by basal area. We ran the analysis for all arborescent life forms (i.e., trees, ferns,
289 and palms) and for trees only, and in all the cases, we excluded lianas from the analysis. The
290 outcome of this analysis indicates the influence of the arboreal life forms, the number and size of
291 stems, and the species composition turnover on plot-level wood density variation along the
292 elevation gradient.

293 To allow biogeographical comparisons of wood density along the elevational gradient,
294 the plots were divided into five different forest types corresponding to those existing in the
295 literature (Young, 1992; Pennington, Reynel and Daza, 2004): *Lowland* (≤ 500 m; including *terra*
296 *firme*, *floodplain*, and *bamboo dominated*), *submontane* (500–1500 m), *lower montane* (1500–
297 2500 m), *upper montane* (2500–3400 m), and *tree line* (≥ 3400 m). Finally, wood density
298 variation was calculated across diameter classes to compare forest structure across forest types.
299 We used ordinary least squares linear regression to explore the intra-and inter-specific
300 relationships between wood density and elevation and the smoothing function of a generalized
301 additive model (GAM) to fit response curves and to test the relationship between wood density
302 and elevation if a non-linear relationship was observed.

303

304 **Results**

305 Across the entire elevational gradient, species mean WD for all arborescent life forms
306 was $0.578 \text{ g cm}^{-3} \pm 0.004$ (95% CI). Focusing on single life forms, the dicot tree species' mean
307 WD was $0.587 \text{ g cm}^{-3} \pm 0.004$ (95% CI), for palms were $0.410 \text{ g cm}^{-3} \pm 0.026$ (95% CI), and for
308 arborescent ferns were $0.351 \text{ g cm}^{-3} \pm 0.003$ (95% CI). The maximum wood density value was
309 1.120 g cm^{-3} for *Machaerium acutifolium* (Fabaceae) in the submontane forest, and the minimum
310 value was 0.111 g cm^{-3} for *Erythrina ulei* (Fabaceae) in the lowland forest. The mean stem-
311 weighted WD for all life forms at the plot level was $0.547 \text{ g cm}^{-3} \pm 0.002$ (95% CI), and the
312 means for trees, palms, and ferns were $0.584 \text{ g cm}^{-3} \pm 0.001$ (95% CI), $0.347 \text{ g cm}^{-3} \pm 0.004$
313 (95% CI) and $0.349 \text{ g cm}^{-3} \pm 0.008$ (95% CI), respectively. Across all elevations, the overall
314 distribution of species and stem-weighted WD for all arborescent life forms and trees alone was
315 symmetric and normal but with a slight positive skewness and kurtosis for species WD and
316 negatively skewed for stem-weighted WD (Supporting information, Fig. S2).

317

318 *Inter- and intra-specific variation of wood density along elevation*

319 Variance partitioning showed that evolutionary relatedness explained most of the variance
320 in wood density for both species sampled in the field (69.4% of the variation) and the plot level,
321 including the 41 forest plots (99.7% of the variation) across the gradient (Fig. S3). The differences
322 among families accounted for the largest proportion of the total variation for the field-sampled
323 species (28.5%), and at the plot level the largest variation was among genera (47.1%; Fig. S3).

324 For the relationship of intraspecific variation in wood density with elevation, 83% of the
325 species sampled ($n = 46$, ≥ 5 individuals) showed no relationship with elevation, and only eight
326 species showed a significant response (Fig. 2a). We found that the modal slope from the

327 regressions was essentially zero [$n = 46$, $\bar{x} = 0.0003 \pm 0.0001$ (95% CI)], with a slight bias toward
328 positive regression slopes (increasing intraspecific wood density with increasing elevation), as
329 compared to negative slopes, with only eight slopes significantly different from zero (Fig. 2a).
330 However, we found large variation between tree species in both the sign and strength of the
331 relationship. For example, wood density in *Clethra cuneata* shows a highly significant decrease
332 with increasing elevation ($n = 45$, $F_{1,43} = 18.44$, adj. $R^2 = 0.28$, $p < 0.0001$; Fig. 2b), whereas
333 *Morella pubescens* ($n = 20$, $F_{1,18} = 2.90$, adj. $R^2 = 0.09$, $p = 0.11$; Fig. 2c) and *Weinmannia bangii*
334 ($n = 26$, $F_{1,24} = 0.0004$, adj. $R^2 = 0.00$, $p = 0.98$; Fig. 2d) had no relationship with elevation. The
335 wood density of *Alnus acuminata* ($n = 17$, $F_{1,15} = 7.75$, adj. $R^2 = 0.30$, $p = 0.013$; Fig. 2e) and
336 *Weinmannia fagaroides* both increased significantly with increasing elevation ($n = 28$, $F_{1,26} =$
337 10.55 , adj. $R^2 = 0.26$, $p = 0.003$; Fig. 2f).

338

339 *Plot-level wood density variation along the elevational gradient*

340 Across the Andes-to-Amazon gradient, plot-to-plot mean wood density showed a non-
341 linear relationship with elevation (Fig. 3, Table S1, Fig. S4). Species mean WD for all arborescent
342 life forms decreased slightly from 190 to 1500 m and remained constant from 1500 to 2500 m,
343 subsequently increased linearly up to the tree line at ~3650 m (Fig. 3a). This trend was different
344 when considering only tree species, with wood density decreasing from 190 to 1500 m and linearly
345 increasing above cloud base up the tree line; palms and fern species mean wood density did not
346 show a relationship with elevation (Fig. 3b, S5). Stem-weighted WD for all arborescent life forms
347 remained constant until 2000 m, declined abruptly between 2250 and 2500 m, and then increased
348 with elevation (Fig. 3c). This trend changed for trees only, with stem-weighted WD slightly
349 declining until the cloud base and then increasing up to the tree line (Fig. 3d). Palm and fern stem-

350 weighted WD were not related to elevation (Fig. 3d, S5). The influence of life forms on plot-level
351 mean wood density variability was driven at middle elevations by arborescent ferns and by palms
352 in lowland sites (Fig. 3, Table S1). When mean species level wood density was weighted by basal
353 area, weighted species mean WD for all arborescent life forms showed lower values, and the stem-
354 weighted WD for trees showed a stronger non-linear relationship of wood density with elevation
355 (Fig. 4a, b), with the lowest values recorded in the submontane forest (Fig. 4b). Species mean
356 wood densities obtained using genus- and family-level identification were highly correlated with
357 those using species-level data ($p < 0.0001$, $r = 0.94$; $p < 0.0001$, $r = 0.89$ respectively; Fig. S6).

358 We observed that plot-to-plot wood density distributions and their statistical moments
359 varied across elevation for both species and stem-weighted WD (Fig. 5). The species WD
360 skewness did not show a clear pattern from low to high elevations. However, the skew was more
361 pronounced at the middle and low elevations for stem-weighted WD, indicating a clear influence
362 of the abundance of low wood density taxa (Fig. 5; Table S2). Mean wood density differs
363 significantly among forest types at the species and stem level (Fig. 6 a-b), but the difference for
364 stem-weighted WD for all arborescent life forms was not significant among life zones along the
365 gradient (Fig. 6 c-d; Kruskal-Wallis, $n = 7$; species WD for all arborescent life forms, $\chi^2 = 16.19$,
366 $p = 0.013$; for trees, $\chi^2 = 15.35$, $p = 0.018$; stem-weighted WD for all arborescent life forms, $\chi^2 =$
367 11.62 , $p = 0.071$; for trees, $\chi^2 = 15.67$, $p = 0.016$). For all taxa, species mean WD was lower at low
368 elevations, reaching a minimum below cloud base in submontane forests and increasing through
369 tree lines for all life forms and trees alone (Fig 6a, b). Stem-weighted WD remained constant
370 toward the lower montane forest and increased only in the upper and tree line forests. When growth
371 form was restricted to just trees, the pattern shifts, with a distinct drop in wood density in

372 submontane forests and wood density exceeding its lowland values only in upper-montane and
373 tree line forests (Fig. 6c, d).

374

375 *Wood density and forest structure*

376 Although the relationship between wood density and DBH class varies greatly among
377 forest types along the gradient, we observed a general tendency where mean wood density
378 decreases with DBH across forest types, and that trend was significant in the submontane ($n = 5$,
379 $F_{1,3} = 22.46$, adj. $R^2 = 0.84$, $p = 0.018$) and lower montane ($n = 5$, $F_{1,3} = 12.69$, adj. $R^2 = 0.74$, $p =$
380 0.037) forests (Fig. 7a). Only in the bamboo-dominated forest mean wood density increased across
381 DBH classes (Fig. 7a). The relationship of mean wood density and DBH classes follow different
382 patterns across the elevation and between the forest plots with stark variability for big trees over
383 50 cm DBH in lowlands (floodplain and terra firme forests) and lower montane forests plots (Fig.
384 7b).

385

386 **Discussion**

387 Mean wood density changes substantially from lowlands to montane environments across
388 the Andes-to-Amazon elevational gradient. Plot-level mean wood density showed a clear non-
389 linear relationship with elevation, and that pattern is explained by changes in species
390 composition and species sorting based on local conditions rather than any general direct effect of
391 elevation *per se*, with intraspecific variation in wood density being absent or showing no
392 consistent trend with elevation. We observed that most of the wood density variation was a result
393 of among-species differences and differences in the community composition because of changes
394 in the relative abundances of different arborescent life forms rather than any within-species

395 variability across the elevational gradient. Moreover, the abundance and distribution of
396 arborescent ferns and palms had a large effect on mean wood density values along the gradient,
397 decreasing wood density by 21% in montane forests dominated by tree ferns and 16% in lowland
398 forests dominated by palms. When looking at community-level changes, the means and
399 distributions of wood density differed greatly depending on whether species were weighted
400 equally or whether wood density values were weighted by individual (community-weighted
401 mean density). To better understand community-level functional traits and their ecological
402 importance, species lists from plots by themselves are not enough, and they need to be combined
403 with the number of individuals and stem size (basal area).

404

405 *Non-linear relationship of increasing wood density with elevation*

406 The present study provides a new framework to understand how wood density varies at
407 species and stem levels across forest types and along a broad elevational gradient. In contrast to
408 the current study, a previous study suggested that wood density significantly decreased with
409 increasing elevation (Chave *et al.*, 2006). The discrepancy could be because Chave *et al.* (2006)
410 only evaluated wood density from 0 to 2500 m rather than the entire Andes-to-Amazon gradient
411 spanning 190 to 3650 m of elevation. Although species mean wood density declines slightly with
412 increasing elevation up to ~1500 m, it increases above that up to the tree line (Fig. 3, 6).

413 The non-linear relationship between wood density and elevation (Fig. 3) is the result of
414 species composition turnover and environment filtering of life histories based on wood density or
415 traits associated with wood density rather than a physiological response (intraspecific variation)
416 to the elevation gradient, which is reflected in the decrease of the distributional variance with
417 increasing elevation at species- and stem-weighted WD (Table S2). The variation in species

418 mean WD resides predominately at genus- and family-level, and that variation principally occurs
419 between rather than within genera and families (Fig. S3), indicating that wood density is highly
420 conserved phylogenetically (Chave *et al.*, 2006; Swenson and Enquist, 2007). The same
421 phylogenetic pattern has been found for leaf mass per area measured from forest canopies across
422 an Andean elevational gradient (Neyret *et al.*, 2016), as well as a large suite of leaf functional
423 traits (G. P. Asner *et al.*, 2014), demonstrating that a wide range of plant functional traits is
424 evolutionarily conserved. We know this is true for individual traits but understanding the
425 correlated suites of traits—the covariances among them—would give information about the
426 major axes of variation or syndromes of functional traits if they do exist (Asner *et al.*, 2016; Díaz
427 *et al.*, 2016). This is important in understanding the effects of environmental filtering and lineage
428 sorting in shaping functional trait patterns across environmental gradients and raises questions
429 about the relative influences of historical (e.g., Andean uplift) and ecological forces in shaping
430 functional traits variation in tropical forests (Chave *et al.*, 2006).

431

432 *Wood properties and the increase of wood density with elevation*

433 Whereas wood density is taken as a comprehensive functional trait, wood has many
434 functions and properties, and only some of them are correlated with density. For instance, non-
435 lumen tissue, such as vessel walls, fibers, and parenchyma, only explain 15% of the variation in
436 wood density, and vessel lumen fraction is unrelated to wood density (Zanne *et al.*, 2010)—what
437 selective forces drive vessel and fiber trait variation remains unclear. Colder environments are
438 potentially dominated by taxa that contain small vessels and tracheids that probably evolved
439 before climate occupancy (Tyree and Zimmermann, 2002; Zanne *et al.*, 2014). Forests at tree
440 lines are exposed to air temperatures below 0 °C and can reach ≤ -5 °C in the austral dry season

441 (June), exposing plants to freezing conditions (Rapp and Silman, 2012). Thus, it is expected that
442 these taxa will contain numerous but short vessels with narrow diameters (Wheeler, Baas and
443 Rodgers, 2007) and thick-walled fibers and vessels (Chave *et al.*, 2009) explaining the high
444 wood density values at higher elevations. In addition, wood density has shown an evolutionary
445 correlation with other plant traits. For instance, wood density decreases with increasing leaf size
446 but was found to be generally unrelated to other functional traits such as seed size, fruit size, and
447 plant height (Wright *et al.*, 2007). However, there are mixed findings for the wood density and
448 leaf mass per area (LMA) relationship, showing either a positive relationship (Ishida *et al.*, 2008)
449 or none at all (Wright *et al.*, 2007). Along a tropical elevational gradient, LMA increases linearly
450 with increasing elevation (Asner *et al.*, 2016), suggesting a positive relationship between wood
451 density and LMA in the Manu-Tambopata elevational transect, although this remains untested.
452 The complex relationships between wood and leaf function remain unclear but are important to
453 understanding the leaf-wood construction costs in the plant growth spectrum between
454 conservative and acquisitive species.

455

456 *Dominant taxa and life forms control wood density variation across the gradient*

457 The role of dominant taxa and arborescent life forms impacts the observed patterns of
458 stem-weighted WD variation across the gradient (Fig. 3, 5, 6). Trends of species and stem-
459 weighted WD with elevation for all arborescent life forms were highly nonlinear (deviance
460 explained = 57.5% for species and 36.4% for stem-weighted WD; Fig. 3a c, S5), and this
461 relationship is even stronger for stem-weighted WD when palms and ferns are excluded
462 (deviance explained = 39.7%; Fig. 3d, S5). The non-linear but positive relationship between
463 wood density and elevation can be explained by the increase in the dominance of heavily

464 wooded species at higher elevations (sensu Slik et al., 2010). More generally, forests at the tree
465 line are dominated by taxa with higher wood density than their lowland counterparts, with lowest
466 values at middle elevations (Figs. 3, 5, 6). For instance, the ten most dominant species at our
467 highest plot in the tree line (e.g., *Miconia alpina*, 0.740 g cm⁻³) account for 17% of the total
468 species but hold 70% of the total stems. This indicates that the highest values of stem-weighted
469 WD at higher elevations (Figs. 3 c, d) are driven by a few dominant heavy-wooded species.
470 Contrasting with the montane pattern, in the Amazonian floodplain forest, the ten most dominant
471 species (e.g., *Iriartea deltoidea* 0.265 g cm⁻³), even though accounting for only 2% of the total
472 species, they account for 38% of the total stems. If we exclude these dominant species, mean
473 wood density values of the floodplain forests show a nonsignificant increase from 0.522 to 0.557
474 g cm⁻³ (Mann-Whitney-Wilcoxon test, n = 6, p = 0.132). This suggests that the abundance of
475 these few species could explain the lower mean stem-weighted WD found in floodplains and, in
476 general, in lowland forests. The plot-level variability in mean species and stem-weighted WD in
477 the Amazonian forest (Fig. 3, 6) can also be associated with the difference in the geomorphology
478 between the Holocene (floodplain) and Pleistocene (terra firme) sediments (Phillips *et al.*, 2019).

479 Whereas general trends in mean wood density values were clear across the elevation
480 gradient, there is substantial variability within any elevation, and much of this variation can be
481 accounted for by the abundance of different arborescent life forms. Dicot trees were the
482 dominant group along the gradient; however, arborescent ferns (i.e., Cyatheaceae and
483 Dicksoniaceae) and palms (i.e., Areaceae) had large effects on mean plot wood density
484 variation in lower montane and lowland forests (Figs. 3, 5, S5). For example, the abrupt decline
485 of mean stem-weighted WD in the submontane and lower montane forests (Figs. 3 a,c; 5; 6 a,c)
486 in the Manu-Tambopata elevational transect is explained by the high abundance of ferns (mean

487 wood density 0.35 g cm^{-3}) at middle elevations. Excluding the dominance of arborescent ferns in
488 the montane forest, mean stem-weighted WD significantly increases from 0.542 to 0.585 g cm^{-3}
489 (Mann-Whitney-Wilcoxon test, $n = 13$, $p = 0.04$), but that difference is pronounced in some sites,
490 for example in TRU-05 and TRU-06 plots, where arborescent ferns comprise 52% and 48% of
491 the total stems at each plot, respectively, resulting in a 24% (for TRU-05) and 20% (for TRU-06)
492 difference in stem-weighted WD as opposed to unweighted WD (Table S1). The same fern
493 abundance patterns at the plot level were found at middle elevations in the Costa Rica elevational
494 transect (Lieberman *et al.*, 1996), indicating that the high abundance of this functional group has
495 important effects on forest structure that translates to the carbon cycle in Neotropical montane
496 forests.

497

498 *The lowest wood density and forest disturbance*

499 Arborescent life forms have profound effects on the wood density variation across the
500 elevation gradient, but this does not fully explain why wood density is lower in mid-montane
501 forests near the cloud base. Excluding non-tree life forms, plot-to-plot wood density variation in
502 true trees (those with secondary xylem) still follows the non-linear relationship along the
503 gradient (Fig. 3, 6; S5). Forest dynamics in tropical mountains are highly influenced by natural
504 disturbances with significant effects on the forest structure, diversity, and function (Crausbay and
505 Martin, 2016). Landslides and tree gaps may be the primary driving forces for vegetation
506 turnover and changes in tree species composition in Andean tropical mountains. Accordingly, a
507 plausible explanation for the consistent trends of lower values of mean wood density at middle
508 elevations around the cloud base may be due to the effects of landslide occurrence. It has been
509 shown that high landslide probability occurs at ~ 1500 m of elevation (Clark *et al.*, 2015; Freund

510 *et al.*, 2021) just below and including the cloud base—below the cloud immersion zone—in the
511 study area (Halladay, Malhi and New, 2012). These are elevations with exceptionally high
512 rainfall, with rain gauges at the site measuring 6–10.5 m of rain per year at 1400 m and 4–8.8 m
513 yr of precipitation at 1800 m. The size, intensity, and recurrence of landslides around the cloud
514 base may lead to a high tree species turnover, facilitating the establishment of fast-growing
515 species with low wood density (e.g., *Urera caracasana*, 0.180 g cm⁻³ and *Heliocarpus*
516 *americanus*, 0.215 g cm⁻³), resulting in highly dynamic and heterogeneous forests with high
517 abundances of low wood-density species. Even large trees have significantly lower wood density
518 values in the sub and lower montane forests than their lowland and upland counterparts (Fig. 7).
519 The light-woodedness may be due to the demands of establishing on high-turnover and
520 competitive landscapes, but it also may be related to the exceptional quantity of precipitation and
521 clouds and low VPD, making large vessel and light-woodedness possible, even for large trees. A
522 way to differentiate between the hypotheses would be to look at the multivariate trait spectrum
523 and see if other traits associated with regeneration on disturbed landscapes are higher at these
524 elevations. In either case, the relationship between minimum mean community wood density
525 with high landslide frequency may be important in understanding how tree communities are
526 assembled.

527

528 *Ecosystem consequences*

529 Wood density has been suggested to play a key role in understanding ecosystem
530 properties, such as carbon cycling (Zanne *et al.*, 2010), and is considered one of the six
531 functional traits that bridge tree diversity and ecosystem function (Díaz *et al.*, 2016). To improve
532 aboveground carbon estimations in tropical forests, allometric equations now include wood

533 density values to reduce uncertainties because it is critical to capture spatial patterns of carbon
534 dynamics at local and regional scales (Malhi *et al.*, 2006; Phillips *et al.*, 2019). Here, we provide
535 a wood density database to reduce uncertainties in carbon calculations, particularly for Andean
536 montane forests where biomass declines with elevation (Asner *et al.*, 2014; Malhi *et al.*, 2016).
537 Current aboveground biomass estimates across the Amazonian forests include palm communities
538 in their calculations (Asner *et al.*, 2014; Malhi *et al.*, 2006). However, even though tree fern
539 abundance exceeds 50% of stems per hectare in some elevations, they are not included in global
540 tropical forest carbon estimates (Saatchi *et al.*, 2011), excluding their contributions to tropical
541 forest carbon stocks. This reinforces the importance of including all arborescent life forms in
542 global forest biomass calculations.

543 This study provides insights into how wood density variation among functional groups,
544 stem size, and habitats could improve carbon dynamic calculations in tropical forests. The sizes
545 of trees (i.e., stem diameter) are important in biomass calculations, in particular, large rainforest
546 trees that account for 2% of the stems but store up to 40% of aboveground biomass per hectare
547 (Clark and Clark, 1996). In this study, when wood density was weighted by basal area, the values
548 were lower than the unweighted wood density, suggesting the dominance of species with low
549 wood density in large sizes trees (Fig. 4). We also observed that large size trees across the
550 gradient tended to have lower mean wood density values than small size classes in all forest types
551 except for bamboo-dominated forest (Fig. 7, S7). Large trees with the lowest wood density
552 values were coincidentally found in the submontane forest, where the lowest community wood
553 density was reported. This negative correlation between wood density and stem diameter was
554 also found in Thai (Sungpalee *et al.*, 2009) and Panamanian tropical forests (Chave *et al.*, 2004);
555 however, the causality of this trend has yet to be resolved.

556 Even though we have expanded the wood density dataset and the understanding of how
557 wood density varies across a 3.5 km elevation gradient, basic uncertainties remain. Even in the
558 most intensive and taxonomically rigorous surveys of tropical Andean forests, 20–40% of taxa
559 (among different Andean surveys) remain as morphospecies known only at the genus level,
560 hampering regional and biogeographic comparisons as well as the understanding of the
561 evolutionary pressures shaping wood density. However, as more than 65% are identified species,
562 it gives us insights into wood density variation across the Andes-to-Amazon forests and
563 contributes to understanding the effects of wood density (species composition) on ecosystem
564 function in particular when projecting future patterns of carbon dynamics based on projected
565 climate changes.

566 **References**

567 ABERG PlotData (2020) ‘Permanent forest plot network’, <http://www.andesconservation.org/>
568 [Preprint].

569 Adler, P.B. *et al.* (2014) ‘Functional traits explain variation in plant life history strategies’,
570 *Proceedings of the National Academy of Sciences*, 111(2), pp. 740–745. Available at:
571 <https://doi.org/10.1073/pnas.1315179111>.

572 Asner, G. P. *et al.* (2014) ‘Landscape-scale changes in forest structure and functional traits along
573 an Andes-to-Amazon elevation gradient’, *Biogeosciences*, 11(3), pp. 843–856. Available at:
574 <https://doi.org/10.5194/bg-11-843-2014>.

575 Asner, Gregory P. *et al.* (2014) ‘Targeted carbon conservation at national scales with high-
576 resolution monitoring’, *Proceedings of the National Academy of Sciences*, 111(47), pp. E5016–
577 E5022. Available at: <https://doi.org/10.1073/pnas.1419550111>.

578 Asner, G.P. *et al.* (2016) ‘Scale dependence of canopy trait distributions along a tropical forest
579 elevation gradient’, *New Phytologist*, June. Available at: <https://doi.org/10.1111/nph.14068>.

580 Baker, T.R. *et al.* (2004) ‘Variation in wood density determines spatial patterns in Amazonian
581 forest biomass’, *Global Change Biology*, 10(5), pp. 545–562.

582 Boyle, B. *et al.* (2013) ‘The taxonomic name resolution service: an online tool for automated
583 standardization of plant names.’, *BMC bioinformatics*, 14(1), p. 16. Available at:
584 <https://doi.org/10.1186/1471-2105-14-16>.

585 Chase, M.W. *et al.* (2016) ‘An update of the Angiosperm Phylogeny Group classification for the
586 orders and families of flowering plants: APG IV’, *Botanical Journal of the Linnean Society*,
587 181(1), pp. 1–20. Available at: <https://doi.org/10.1111/boj.12385>.

588 Chave, J. *et al.* (2004) ‘Error propagation and scaling for tropical forest biomass estimates’,
589 *Philosophical Transactions of the Royal Society B: Biological Sciences*, 359(1443), pp. 409–420.
590 Available at: <https://doi.org/10.1098/rstb.2003.1425>.

591 Chave, J. *et al.* (2006) ‘Regional and phylogenetic variation of wood density across 2456
592 neotropical tree species’, *Ecological Applications*, 16(6), pp. 2356–2367.

593 Chave, J. *et al.* (2009) ‘Towards a worldwide wood economics spectrum’, *Ecology Letters*,
594 12(4), pp. 351–366. Available at: <https://doi.org/10.1111/j.1461-0248.2009.01285.x>.

595 Clark, D.B. and Clark, D.A. (1996) ‘Abundance, growth and mortality of very large trees in
596 neotropical lowland rain forest’, *Forest Ecology and Management*, 80(1–3), pp. 235–244.
597 Available at: [https://doi.org/10.1016/0378-1127\(95\)03607-5](https://doi.org/10.1016/0378-1127(95)03607-5).

598 Clark, K.E. *et al.* (2015) ‘Storm-triggered landslides in the Peruvian Andes and implications for
599 topography, carbon cycles, and biodiversity’, *Earth Surface Dynamics Discussions*, 3(3), pp.
600 631–688. Available at: <https://doi.org/10.5194/esurfd-3-631-2015>.

601 Crausbay, S.D. and Martin, P.H. (2016) ‘Natural disturbance, vegetation patterns and ecological
602 dynamics in tropical montane forests’, *Journal of Tropical Ecology*, 32(05), pp. 384–403.
603 Available at: <https://doi.org/10.1017/S0266467416000328>.

604 Díaz, S. *et al.* (2016) ‘The global spectrum of plant form and function’, *Nature*, 529(7585), pp.
605 167–171. Available at: <http://dx.doi.org/10.1038/nature16489>.

606 Farfan-Rios, W. *et al.* (2015) ‘Lista anotada de árboles y afines en los bosques montanos del
607 sureste peruano : la importancia de seguir recolectando’, *Revista Peruana de Biología*, 22(2), pp.
608 145–174. Available at: <http://dx.doi.org/10.15381/rpb.v22i2.11351>.

609 Fearnside, P.M. (1997) ‘Wood density for estimating forest biomass in Brazilian Amazonia’,
610 *Forest Ecology and Management*, 90(1), pp. 59–87. Available at: [https://doi.org/10.1016/S0378-](https://doi.org/10.1016/S0378-1127(96)03840-6)
611 1127(96)03840-6.

612 Fortunel, C. *et al.* (2014) ‘Wood specific gravity and anatomy of branches and roots in 113
613 Amazonian rainforest tree species across environmental gradients.’, *The New phytologist*, 202(1),
614 pp. 79–94. Available at: <https://doi.org/10.1111/nph.12632>.

615 Freund, C.A. *et al.* (2021) ‘Landslide age, elevation and residual vegetation determine tropical
616 montane forest canopy recovery and biomass accumulation after landslide disturbances in the
617 Peruvian Andes’, *Journal of Ecology*, 109(10), pp. 3555–3571. Available at:
618 <https://doi.org/10.1111/1365-2745.13737>.

619 Fyllas, N.M. *et al.* (2017) ‘Solar radiation and functional traits explain the decline of forest
620 primary productivity along a tropical elevation gradient’, *Ecology Letters*. Edited by Dr.N.
621 Swenson, 20(6), pp. 730–740. Available at: <https://doi.org/10.1111/ele.12771>.

622 Gentry, A. (1995) ‘Patterns of diversity and floristic composition in neotropical montane
623 forests’, in S.P. Churchill *et al.* (eds) *Biodiversity and Conservation of Neotropical Montane*
624 *Forests: Proceedings of the Neotropical Montane Forest Biodiversity and Conservation*
625 *Symposium*. New York.: New York Botanical Garden, pp. 103–126.

626 Halladay, K., Malhi, Y. and New, M. (2012) ‘Cloud frequency climatology at the
627 Andes/Amazon transition: 1. Seasonal and diurnal cycles’, *J. Geophys. Res.*, 117, pp. D23102,
628 doi:10.1029/2012JD017770.

629 von Humboldt, A. (1838) *Notice de Deux Tentatives d’Ascension du Chimborazo (A. Pihan de la*
630 *Forest, Paris)*.

631 Ishida, A. *et al.* (2008) ‘Coordination between leaf and stem traits related to leaf carbon gain and
632 hydraulics across 32 drought-tolerant angiosperms’, *Oecologia*, 156(1), pp. 193–202. Available
633 at: <https://doi.org/10.1007/s00442-008-0965-6>.

634 King, D.A. *et al.* (2005) ‘Tree growth is related to light interception and wood density in two
635 mixed dipterocarp forests of Malaysia’, *Functional Ecology*, 19(3), pp. 445–453. Available at:
636 <https://doi.org/10.1111/j.1365-2435.2005.00982.x>.

637 Lieberman, D. *et al.* (1996) ‘Tropical forest structure and composition on a large-scale altitudinal
638 gradient in Costa Rica’, *Journal of Ecology*, 84(2), pp. 137–152.

639 Lopez-Gonzalez, G. *et al.* (2011) ‘ForestPlots.net: a web application and research tool to manage
640 and analyse tropical forest plot data’, *Journal of Vegetation Science*, 22(4), pp. 610–613.
641 Available at: <https://doi.org/10.1111/j.1654-1103.2011.01312.x>.

642 Malhi, Y. *et al.* (2006) ‘The regional variation of aboveground live biomass in old-growth
643 Amazonian forests’, *Global Change Biology*, 12(7), pp. 1107–1138.

644 Malhi, Y. *et al.* (2010) ‘Introduction: Elevation gradients in the tropics: laboratories for
645 ecosystem ecology and global change research’, *Global Change Biology*, 16(12), pp. 3171–3175.

646 Malhi, Y. *et al.* (2016) ‘The variation of productivity and its allocation along a tropical elevation
647 gradient: a whole carbon budget perspective’, *New Phytologist* [Preprint]. Available at:
648 <https://doi.org/10.1111/nph.14189>.

649 Messier, J., McGill, B.J. and Lechowicz, M.J. (2010) ‘How do traits vary across ecological
650 scales? A case for trait-based ecology’, *Ecology Letters*, 13(7), pp. 838–848. Available at:
651 <https://doi.org/10.1111/j.1461-0248.2010.01476.x>.

652 Muller-Landau, H.C. (2004) ‘Interspecific and Inter-site Variation in Wood Specific Gravity of
653 Tropical Trees’, *Biotropica*, 36(1), pp. 20–32. Available at: [https://doi.org/10.1111/j.1744-](https://doi.org/10.1111/j.1744-7429.2004.tb00292.x)
654 [7429.2004.tb00292.x](https://doi.org/10.1111/j.1744-7429.2004.tb00292.x).

655 Neyret, M. *et al.* (2016) ‘Examining variation in the leaf mass per area of dominant species
656 across two contrasting tropical gradients in light of community assembly’, *Ecology and*
657 *Evolution*, 6(16), pp. 5674–5689. Available at: <https://doi.org/10.1002/ece3.2281>.

658 Pennington, T.D., Reynel, C. and Daza, A. (2004) *Illustrated guide to the Trees of Peru*. Edited
659 by T.D. Pennington, C. Reynel, and A. Daza. Sherborne, UK: David Hunt.

660 Phillips, O.L. *et al.* (2019) ‘Species Matter: Wood Density Influences Tropical Forest Biomass at
661 Multiple Scales’, *Surveys in Geophysics*, pp. 1–23. Available at: [https://doi.org/10.1007/s10712-](https://doi.org/10.1007/s10712-019-09540-0)
662 [019-09540-0](https://doi.org/10.1007/s10712-019-09540-0).

663 Pitman, N.C.A., Silman, M.R. and Terborgh, J.W. (2013) ‘Oligarchies in Amazonian tree
664 communities: A ten-year review’, *Ecography*, 36(2), pp. 114–123. Available at:
665 <https://doi.org/10.1111/j.1600-0587.2012.00083.x>.

666 Poorter, L. *et al.* (2008) ‘Are functional traits good predictors of demographic rates? evidence
667 from five neotropical forests’, *Ecology*, 89(7), pp. 1908–1920. Available at:
668 <https://doi.org/10.1890/07-0207.1>.

669 Putz, F.E. *et al.* (1983) ‘Uprooting and Snapping of Trees - Structural Determinants and
670 Ecological Consequences’, *Canadian Journal of Forest Research-Revue Canadienne De
671 Recherche Forestiere*, 13(5), pp. 1011–1020.

672 Rapp, J.M. and Silman, M.R. (2012) ‘Diurnal, seasonal, and altitudinal trends in microclimate
673 across a tropical montane cloud forest’, *Climate Research*, 55(1), pp. 17–32. Available at:
674 <https://doi.org/10.3354/cr01127>.

675 Ruger, N. *et al.* (2012) ‘Functional traits explain light and size response of growth rates in
676 tropical tree species’, *Ecology*, 93(12), pp. 2626–2636. Available at: [https://doi.org/10.1890/12-](https://doi.org/10.1890/12-0622.1)
677 [0622.1](https://doi.org/10.1890/12-0622.1).

678 Saatchi, S.S. *et al.* (2011) ‘Benchmark map of forest carbon stocks in tropical regions across
679 three continents.’, *Proceedings of the National Academy of Sciences of the United States of
680 America*, 108(24), pp. 9899–904. Available at: <https://doi.org/10.1073/pnas.1019576108>.

681 Silman, M.R. (2014) ‘Functional megadiversity.’, *Proceedings of the National Academy of
682 Sciences of the United States of America*, 111(16), pp. 5763–4. Available at:
683 <https://doi.org/10.1073/pnas.1402618111>.

684 Slik, J.W.F. *et al.* (2010) ‘Environmental correlates of tree biomass, basal area, wood specific
685 gravity and stem density gradients in Borneo’s tropical forests’, *Global Ecology and*

686 *Biogeography*, 19(1), pp. 50–60. Available at: <https://doi.org/10.1111/j.1466->
687 8238.2009.00489.x.

688 Sperry, J.S., Meinzer, F.C. and McCulloh, K.A. (2008) ‘Safety and efficiency conflicts in
689 hydraulic architecture: scaling from tissues to trees.’, *Plant, cell & environment*, 31(5), pp. 632–
690 45. Available at: <https://doi.org/10.1111/j.1365-3040.2007.01765.x>.

691 ter Steege, H. *et al.* (2006) ‘Continental-scale patterns of canopy tree composition and function
692 across Amazonia’, *Nature*, 443(7110), pp. 444–447. Available at:
693 <https://doi.org/10.1038/nature05134>.

694 ter Steege, H. *et al.* (2013) ‘Hyperdominance in the Amazonian tree flora.’, *Science (New York,*
695 *N.Y.)*, 342(6156), p. 1243092. Available at: <https://doi.org/10.1126/science.1243092>.

696 Sungpalee, W. *et al.* (2009) ‘Intra- and interspecific variation in wood density and fine-scale
697 spatial distribution of stand-level wood density in a northern Thai tropical montane forest’,
698 *Journal of Tropical Ecology*, 25(04), pp. 359–370. Available at:
699 <https://doi.org/doi:10.1017/S0266467409006191>.

700 Swenson, N.G. and Enquist, B.J. (2007) ‘Ecological and evolutionary determinants of a key
701 plant functional trait: wood density and its community-wide variation across latitude and
702 elevation.’, *American journal of botany*, 94(3), pp. 451–9. Available at:
703 <https://doi.org/10.3732/ajb.94.3.451>.

704 Tyree, M.T. and Zimmermann, M.H. (2002) ‘Hydraulic Architecture of Whole Plants and Plant
705 Performance’, in *Springer*. Springer, Berlin, Heidelberg, pp. 175–214. Available at:
706 https://doi.org/10.1007/978-3-662-04931-0_6.

707 Vasquez M., R. and Rojas G., R.D.P. (2016) *Clave para identificar grupos de familias de*
708 *Gymnospermae y Angiospermae del Perú*. Jardin Botanico de Missouri.

709 Wheeler, E.A., Baas, P. and Rodgers, S. (2007) ‘Variations in dicot wood anatomy: A global
710 analysis based on the insidewood database’, *IAWA Journal*. Brill, pp. 229–258. Available at:
711 <https://doi.org/10.1163/22941932-90001638>.

712 Williamson, G.B. (1984) ‘Gradients in Wood Specific Gravity of Trees’, *Bulletin of the Torrey*
713 *Botanical Club*, 111(1), pp. 51–55. Available at: <https://doi.org/10.2307/2996210>.

714 Williamson, G.B. and Wiemann, M.C. (2010) ‘Measuring wood specific gravity...correctly’,
715 *American Journal of Botany*, 97(3), pp. 519–524. Available at:
716 <https://doi.org/10.3732/ajb.0900243>.

717 Wright, I.J. *et al.* (2007) ‘Relationships among ecologically important dimensions of plant trait
718 variation in seven neotropical forests’, *Annals of Botany*, 99(5), pp. 1003–1015. Available at:
719 <https://doi.org/10.1093/aob/mcl066>.

720 Young, K.R. (1992) ‘Biogeography of the montane forest zone of the eastern slopes of Peru’,
721 *Memorias del Museo de Historia Natural U.N.M.S.M.*, 21, pp. 119–154.

722 Zanne, A.E. *et al.* (2009) ‘Data from: Towards a worldwide wood economics spectrum’, *Ecology*
723 *Letters* [Preprint]. Dryad Data Repository. Available at: <http://dx.doi.org/10.5061/dryad.234>.

724 Zanne, A.E. *et al.* (2010) ‘Angiosperm wood structure: Global patterns in vessel anatomy and
725 their relation to wood density and potential conductivity.’, *American journal of botany*, 97(2),
726 pp. 207–15. Available at: <https://doi.org/10.3732/ajb.0900178>.

727 Zanne, A.E. *et al.* (2014) ‘Three keys to the radiation of angiosperms into freezing
728 environments.’, *Nature*, 506(7486), pp. 89–92. Available at:
729 <https://doi.org/10.1038/nature12872>.

730 **Figure legends:**

731 **Figure 1.** Location of the 51 wood collection sites (red circles) and the 41 permanent forest plots
732 (yellow squares) on the eastern slope of the Peruvian Andes along an elevational gradient
733 extending from the tree line at 3700 m to the Amazon basin at 190 m.

734
735 **Figure 2.** (a) Empirical distribution of within-species slopes of the linear regression between
736 wood density and elevation ($n = 46$)—vertical bars represent the slopes significantly different
737 from zero (8 positives and 1 negative). Intraspecific variation in wood density across elevations
738 for (b) *Clethra cuneata* ($n = 45$), (c) *Morella pubescens* ($n = 20$), (d) *Weinmannia bangii* ($n =$
739 26), (e) *Alnus acuminata* ($n = 17$), and (f) *Weinmannia fagaroides* ($n = 28$). Gray circles
740 represent sampled individuals across elevation, black circles represent the mean wood density
741 among species at each sampled site. The black solid line represents the linear regression fit with
742 95% confidence limits. Error bars depict bootstrapped 95% confidence intervals.

743
744 **Figure 3.** Plot-level mean wood density variation across 41 permanent forest plots along the
745 Andes-to-Amazon elevational gradient for (a) species mean wood density for all arborescent life
746 forms and (b) for trees, palms, and ferns species. (c) Stem-weighted mean wood density for all
747 arborescent life forms and (d) for trees, palms, and ferns. Error bars depict bootstrapped 95%
748 confidence intervals. Solid lines are generalized additive models (GAM) fit using a smoothing

749 function with 95% confidence limits. Vertical dashed lines represent the approximate elevation
750 of the cloud base.

751
752 **Figure 4.** (a) Species mean wood density for all arborescent life forms and trees. (b) Species
753 mean wood density for all arborescent life forms and trees weighted by basal area. Open
754 triangles represent all arborescent life forms, and gray circles represent trees. Solid and dashed
755 lines are generalized additive models (GAM) fit using a smoothing function. Vertical dashed
756 lines represent the position of the cloud base along the gradient. Legend corresponds to the same
757 life forms for panels (a) and (b).

758
759 **Figure 5.** Wood density distribution for species (blue lines) and stems (red lines) for all plots (n
760 = 41) across the Andes-to-Amazon elevational gradient. Data include all arborescent life forms.
761 Vertical dashed lines indicate corresponding means.

762
763 **Figure 6.** Plot-level wood density variation across forests types including: Lowland (Ltf =
764 Lowland terra firme, Lfp = Lowland floodplain, Lbb = Lowland bamboo dominated forest; <500
765 m), submontane (SM: 500–1500 m), lower montane (LM: 1500–2500 m), upper montane (UP:
766 2500–3400 m) and tree line (TL: >3400 m) for (a) species mean WD including all arborescent
767 life forms and (b) tree species. (c) Stem-weighted WD for all arborescent life forms and (d) tree
768 stems. Box plots show 25% quartile, median, and 75% quartile of the distribution (horizontal
769 lines). Forest types are defined based on Young (1992) and Pennington et al. (2004).

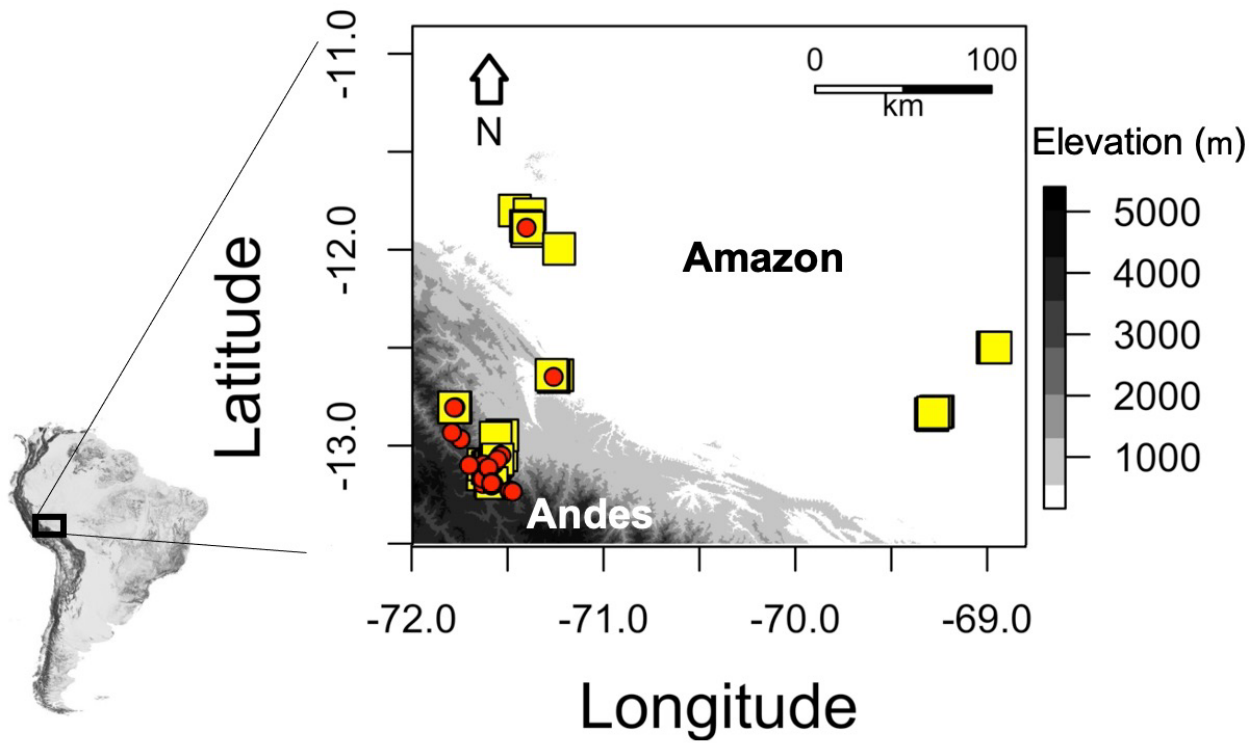
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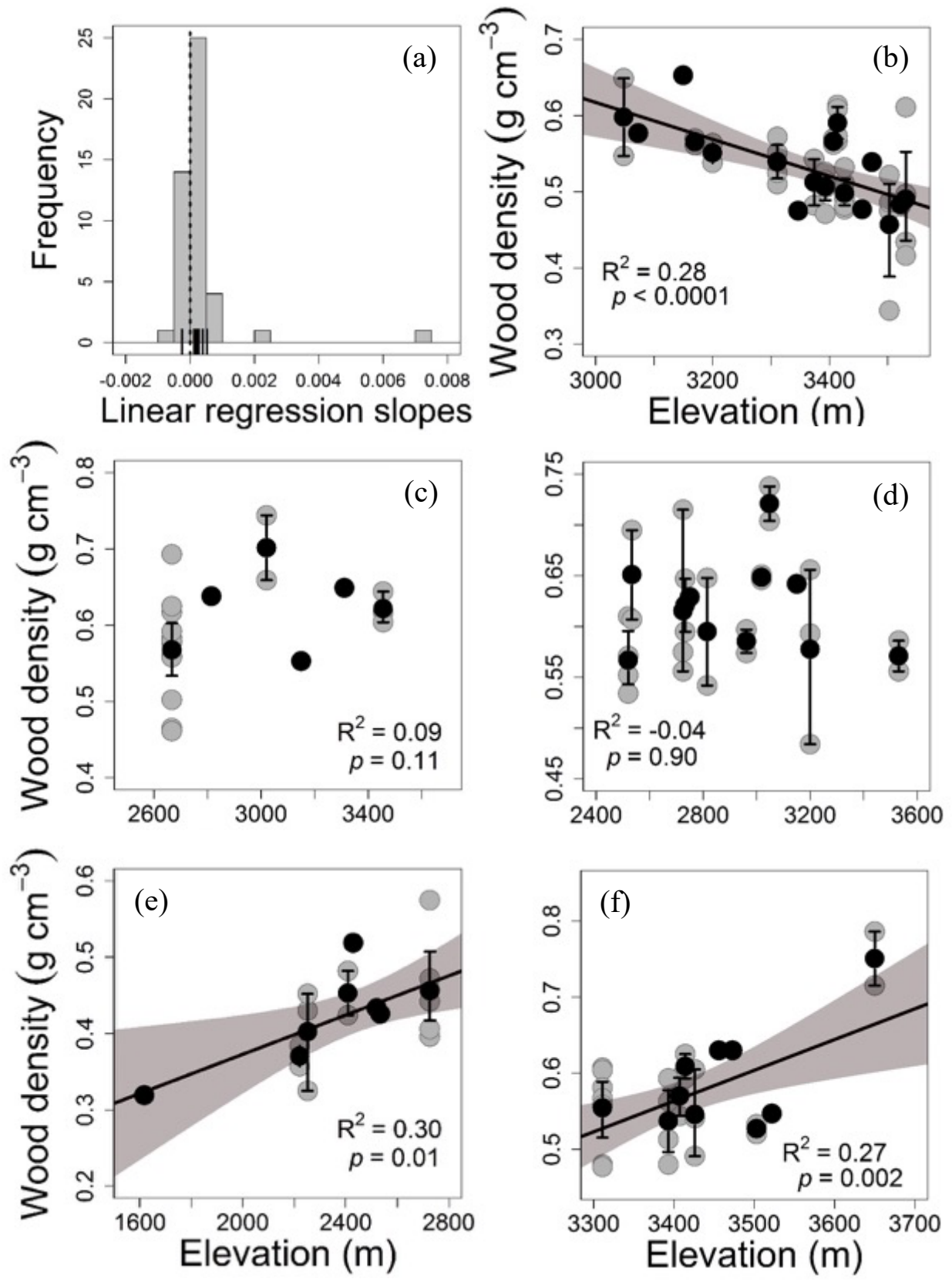
771 **Figure 7.** (a) Mean wood density variation for individual stems across DBH classes. Regression
772 lines were computed using the mean averaged wood density across diameter classes for each
773 forest type. Stars represent significant relationships. (b) Coefficient of variation (CV) of wood
774 density across diameter classes—CV was calculated using the mean averaged wood density
775 across diameter classes for each forest type. Color lines correspond to the same forest types for
776 both (a) and (b).

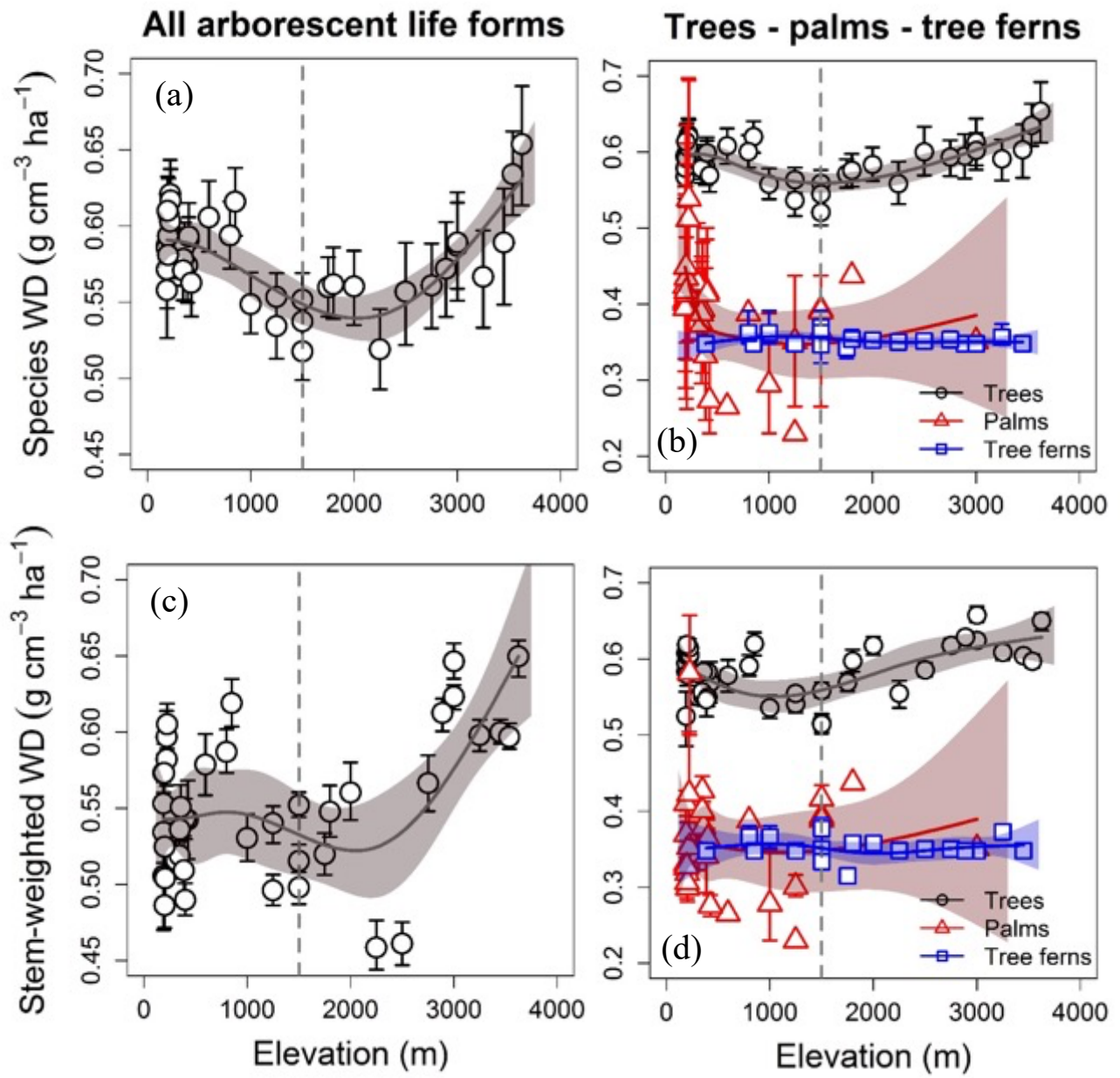
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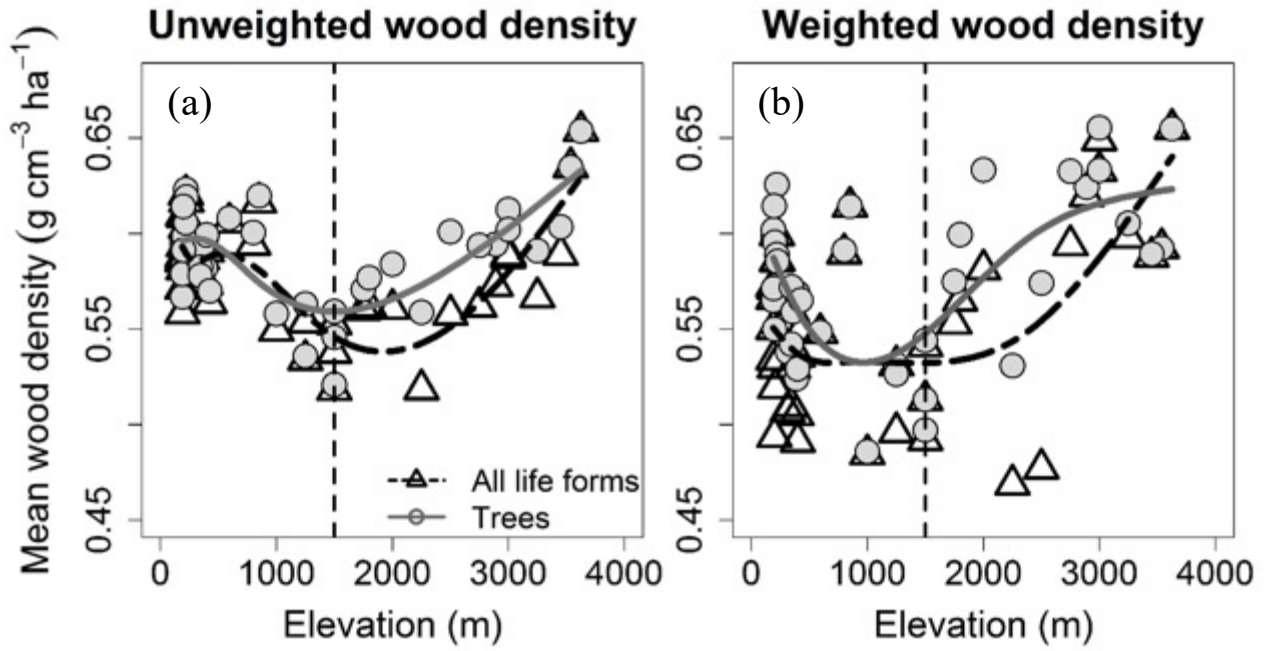
778 **Figure 8.** Mean wood density and landslide stability (LS) as a function of elevation along the
779 Andes-to-Amazon transect. LS was calculated as the inverted scale of landslide probability (1-
780 landslide probability [%yr⁻¹]) taken from Clark et al. (2015). Species mean wood density
781 includes (a) all arborescent life forms and (b) trees only. Vertical dashed lines represent the cloud
782 base in the gradient. Open circles represent mean species wood density and gray triangles
783 landslide stability.

784 **Figure 1.**

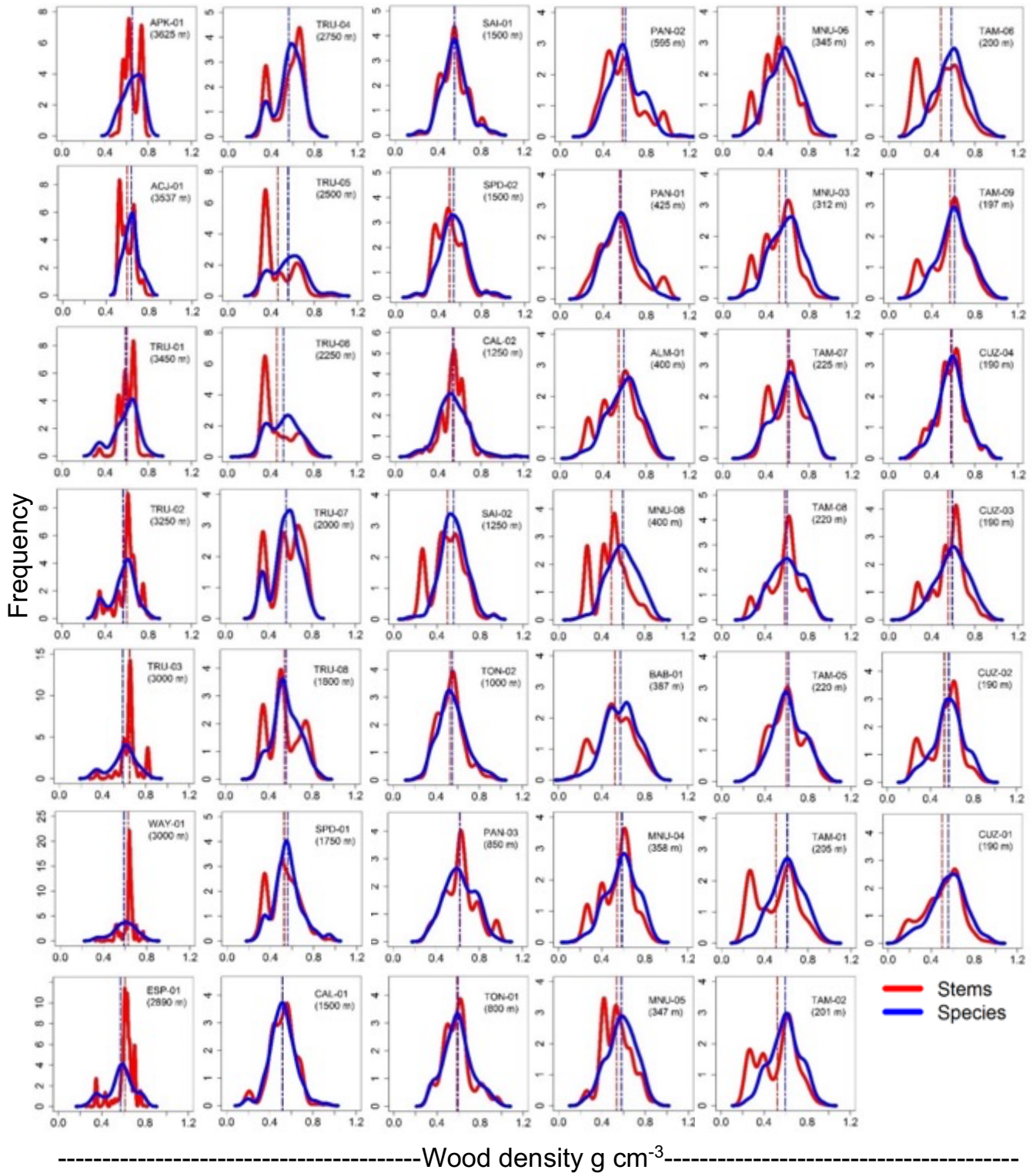


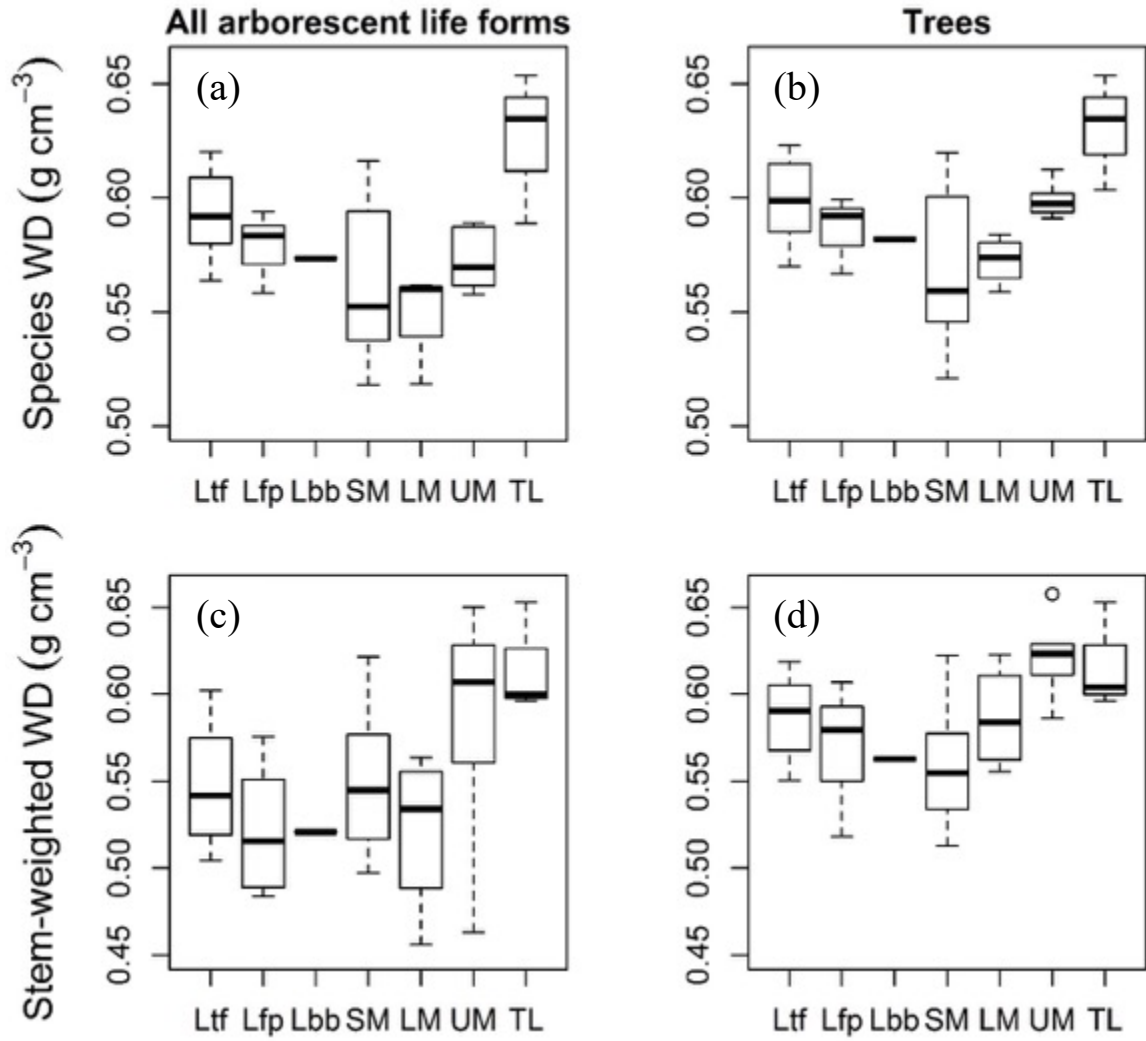


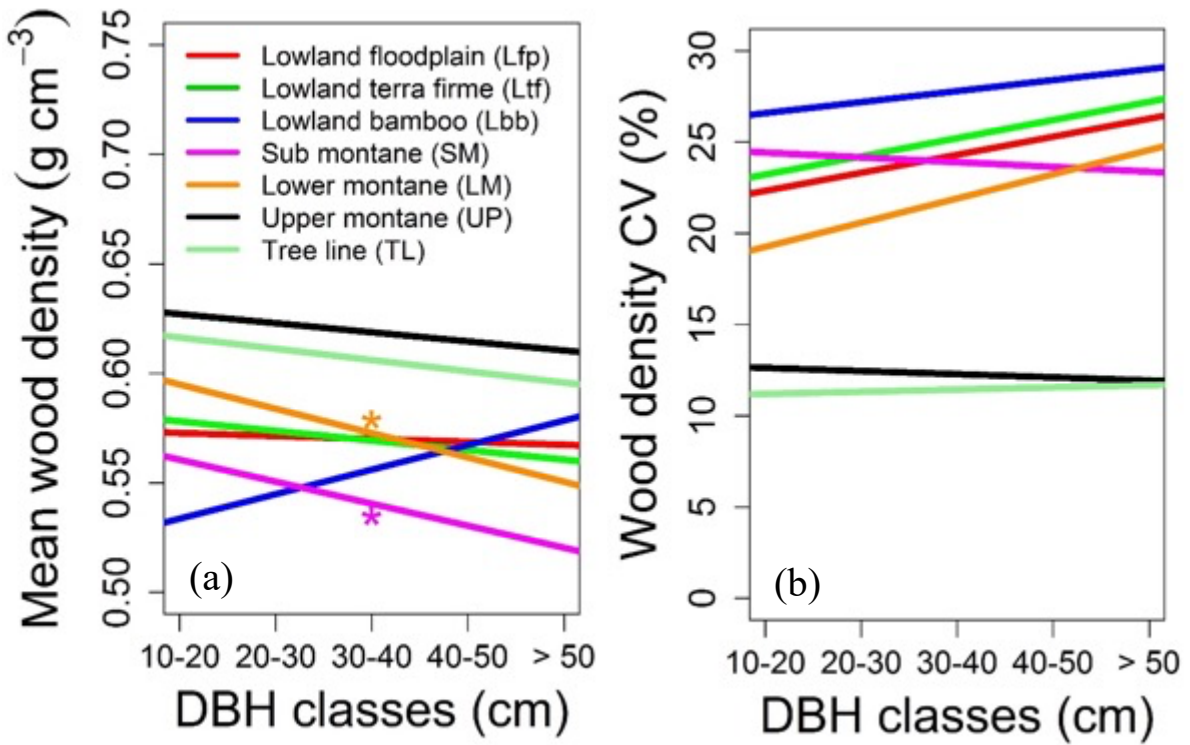




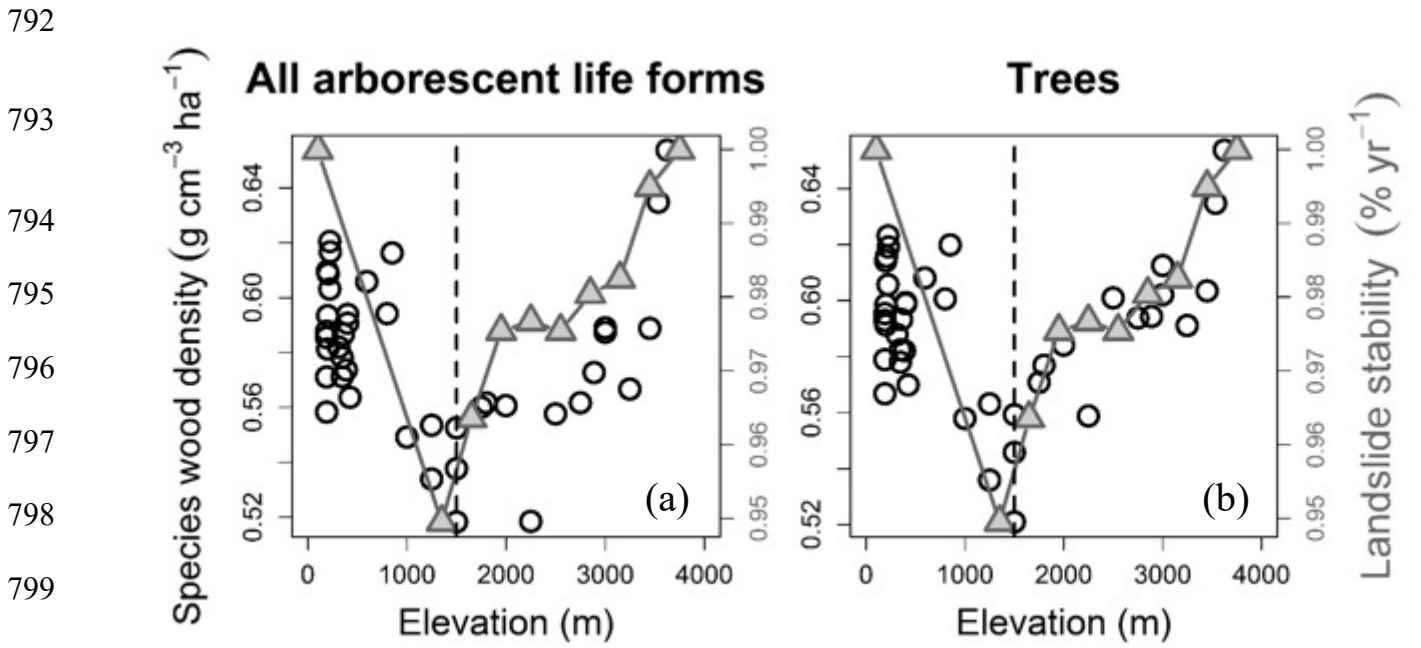
788 **Figure 5.**







791 **Figure 8.**



805 **Supporting Information**

806

807

808 **Article title:** Wood density variation across an Andes-to-Amazon elevational gradient

809

810

811 **Results**

812 Across all elevations, the overall distribution of species mean Wood Density (WD) for all
813 arborescent life forms and trees alone was symmetric and normal with a slight positive skewness
814 and kurtosis (all life forms: Skewness = 0.07, kurtosis = 2.96; trees: Skewness = 0.09, kurtosis =
815 3.1). Likewise, the distribution of stem-weighted mean wood density for all arborescent life
816 forms and for trees alone were symmetric and normal but were negatively skewed with positive
817 kurtosis for both, all arborescent (skewness = -0.18, kurtosis = 2.70) and tree stems (skewness =
818 -0.13, kurtosis = 3.53) (Fig. S2).

819

820 Plot-to-plot wood density distributions and their statistical moments varied across elevations.
821 Species WD distributions shifted from a negative skew in the lowlands to a positive skew in the
822 submontane forest and shifted again to a negative skew in the montane to tree line forest plots,
823 with this pattern being similar for all arborescent life forms and trees only (Table S2). The montane
824 and lowland plots showed a negative kurtosis, but we observed a positive kurtosis only in the
825 submontane forest plots (Table S2). For stem WD distributions, we observed a marked increase in
826 the right skew (right tail increasing) in plots with a high abundance of few species with low wood
827 density values in the montane (e.g., TRU-05, TRU-06) and lowland forests plots (e.g., TAM-01,

828 MNU-08; Table S2). Kurtosis for stem WD distributions for all arborescent life forms and only
829 trees varied along the gradient, with the predominance of negative kurtosis in the lowland forests
830 (Table S2).

831 **Table S1.** Site description and mean wood density values for 41 (47.5 ha) forest plots across the Andes-to-Amazon elevational
 832 gradient.

Plot	Elevation (m)	Size (ha)	Forest type	Basal area (m ² ha ⁻¹)				Mean wood density (g cm ⁻³)											
								Species				Stems				Basal area			
				All				All				All				All			
				life		Tree		life		Tree		life		Tree		life		Tree	
forms	Trees	Palms	ferns	forms	Trees	Palms	ferns	forms	Trees	Palms	ferns	forms	Trees	Palms	ferns	forms	Trees	Palms	ferns
APK-01	3625	1	Tree line	21.2	21.2	-	-	0.654	0.654	-	-	0.653	0.653	-	-	0.655	0.655	-	-
ACJ-01	3537	1	Tree line	37.3	37.3	-	-	0.635	0.635	-	-	0.596	0.596	-	-	0.592	0.592	-	-
TRU-01	3450	1	Tree line	28.6	28.4	-	0.2	0.589	0.603	-	0.348	0.600	0.604	-	0.348	0.588	0.589	-	0.348
TRU-02	3250	1	Upper montane	31.2	30.2	-	1.0	0.567	0.591	-	0.357	0.600	0.611	-	0.370	0.598	0.605	-	0.373
TRU-03	3000	1	Upper montane	20.5	20.0	0.0	0.4	0.587	0.612	0.351	0.348	0.650	0.658	0.351	0.348	0.649	0.655	0.351	0.348
WAY-01	3000	1	Upper montane	34.3	34.3	-	0.0	0.589	0.602	-	0.348	0.628	0.629	-	0.348	0.633	0.633	-	0.348
ESP-01	2890	1	Upper montane	28.2	27.7	-	0.5	0.573	0.594	-	0.348	0.614	0.628	-	0.348	0.620	0.624	-	0.348
TRU-04	2750	1	Upper montane	34.7	29.9	-	4.7	0.562	0.594	-	0.353	0.561	0.618	-	0.350	0.594	0.633	-	0.349
TRU-05	2500	1	Upper montane	43.5	24.6	-	18.8	0.558	0.601	-	0.351	0.463	0.586	-	0.350	0.477	0.574	-	0.350
TRU-06	2250	1	Lower montane	37.0	24.4	-	12.6	0.518	0.559	-	0.350	0.456	0.556	-	0.348	0.469	0.531	-	0.348
TRU-07	2000	1	Lower montane	21.0	17.0	-	4.0	0.561	0.584	-	0.353	0.564	0.623	-	0.359	0.581	0.633	-	0.359
TRU-08	1800	1	Lower montane	29.6	25.4	0.1	4.2	0.562	0.577	0.437	0.354	0.547	0.599	0.437	0.358	0.565	0.599	0.437	0.358
SPD-01	1750	1	Lower montane	36.5	33.5	-	3.1	0.560	0.571	-	0.343	0.521	0.569	-	0.316	0.553	0.575	-	0.313

Plot	Elevation (m)	Size (ha)	Forest type	Basal area (m ² ha ⁻¹)				Mean wood density (g cm ⁻³)											
								Species				Stems				Basal area			
				All				All				All				All			
				life		Tree		life		Tree		life		Tree		life		Tree	
forms	Trees	Palms	ferns	forms	Trees	Palms	ferns	forms	Trees	Palms	ferns	forms	Trees	Palms	ferns	forms	Trees	Palms	ferns
CAL-01	1500	1	Submontane	30.8	30.7	0.0	0.0	0.518	0.521	0.393	0.369	0.517	0.517	0.393	0.377	0.513	0.513	0.393	0.376
SAI-01	1500	1	Submontane	41.2	40.4	0.7	0.2	0.552	0.559	0.363	0.362	0.553	0.559	0.414	0.353	0.541	0.544	0.412	0.351
SPD-02	1500	1	Submontane	30.4	29.4	0.1	0.9	0.538	0.546	0.390	0.347	0.499	0.513	0.388	0.332	0.492	0.497	0.388	0.333
CAL-02	1250	1	Submontane	37.0	36.9	0.0	-	0.534	0.536	0.230	-	0.545	0.545	0.230	-	0.531	0.531	0.230	-
SAI-02	1250	1	Submontane	42.2	36.3	5.7	0.2	0.553	0.563	0.351	0.348	0.497	0.555	0.310	0.348	0.496	0.526	0.308	0.348
TON-02	1000	1	Submontane	31.3	31.1	0.1	0.1	0.549	0.558	0.294	0.362	0.529	0.534	0.278	0.364	0.484	0.486	0.257	0.367
PAN-03	850	1	Submontane	24.2	24.2	-	0.0	0.616	0.620	-	0.348	0.622	0.622	-	0.348	0.614	0.614	-	0.348
TON-01	800	1	Submontane	26.5	26.3	0.0	0.2	0.594	0.601	0.388	0.362	0.586	0.589	0.388	0.369	0.590	0.591	0.388	0.370
PAN-02	595	1	Submontane	27.7	27.7	0.0	-	0.606	0.608	0.265	-	0.577	0.577	0.265	-	0.548	0.548	0.265	-
PAN-01	425	1	Lowland (TF)	27.3	25.8	1.4	-	0.564	0.570	0.274	-	0.551	0.577	0.271	-	0.550	0.565	0.271	-
ALM-01	400	2	Lowland (TF)	31.2	26.9	4.3	-	0.591	0.599	0.419	-	0.542	0.580	0.347	-	0.536	0.569	0.327	-
MNU-08	400	2	Lowland (FP)	41.8	33.9	7.9	-	0.594	0.599	0.413	-	0.489	0.550	0.364	-	0.491	0.529	0.328	-
BAB-01	387	1	Lowland (BB)	29.3	26.9	2.4	0.0	0.574	0.582	0.332	0.348	0.521	0.563	0.335	0.348	0.505	0.524	0.289	0.348
MNU-04	358	2	Lowland (TF)	28.2	24.3	3.9	-	0.587	0.593	0.392	-	0.541	0.580	0.365	-	0.530	0.559	0.350	-
MNU-05	347	2.25	Lowland (TF)	30.7	28.6	2.1	-	0.578	0.582	0.373	-	0.536	0.551	0.430	-	0.559	0.572	0.391	-
MNU-06	345	2.25	Lowland (TF)	32.3	27.0	5.3	-	0.571	0.578	0.388	-	0.517	0.559	0.383	-	0.510	0.542	0.350	-

Plot	Elevation (m)	Size (ha)	Forest type	Basal area (m ² ha ⁻¹)				Mean wood density (g cm ⁻³)											
								Species				Stems				Basal area			
				All				All				All				All			
				life		Tree		life		Tree		life		Tree		life		Tree	
forms	Trees	Palms	ferns	forms	Trees	Palms	ferns	forms	Trees	Palms	ferns	forms	Trees	Palms	ferns	forms	Trees	Palms	ferns
MNU-03	312	2	Lowland (TF)	30.3	26.1	4.2	-	0.582	0.588	0.427	-	0.518	0.552	0.340	-	0.507	0.538	0.315	-
TAM-07	225	1	Lowland (TF)	25.5	25.2	0.4	-	0.617	0.619	0.539	-	0.602	0.602	0.588	-	0.586	0.585	0.609	-
TAM-05	220	1	Lowland (TF)	27.6	27.1	0.5	-	0.620	0.623	0.512	-	0.600	0.606	0.436	-	0.585	0.589	0.406	-
TAM-08	220	1	Lowland (TF)	22.2	20.3	2.0	-	0.603	0.606	0.512	-	0.583	0.614	0.360	-	0.599	0.626	0.328	-
TAM-01	205	1	Lowland (TF)	28.8	22.0	6.8	-	0.609	0.616	0.418	-	0.504	0.601	0.292	-	0.519	0.595	0.275	-
TAM-02	201	1	Lowland (TF)	28.1	22.0	6.1	-	0.593	0.599	0.434	-	0.520	0.604	0.315	-	0.530	0.595	0.293	-
TAM-06	200	1	Lowland (FP)	37.6	29.4	8.2	-	0.581	0.591	0.418	-	0.484	0.574	0.292	-	0.493	0.550	0.290	-
TAM-09	197	1	Lowland (TF)	23.3	20.3	3.0	-	0.610	0.614	0.455	-	0.567	0.619	0.298	-	0.571	0.614	0.283	-
CUZ-01	190	1	Lowland (FP)	27.2	25.5	1.7	-	0.558	0.567	0.403	-	0.502	0.518	0.358	-	0.550	0.565	0.333	-
CUZ-02	190	1	Lowland (FP)	27.9	24.0	3.9	-	0.571	0.579	0.405	-	0.529	0.585	0.315	-	0.534	0.571	0.305	-
CUZ-03	190	1	Lowland (FP)	27.7	24.5	3.2	-	0.588	0.595	0.432	-	0.551	0.593	0.327	-	0.566	0.598	0.314	-
CUZ-04	190	1	Lowland (FP)	28.1	24.4	3.6	-	0.585	0.593	0.405	-	0.576	0.607	0.409	-	0.572	0.602	0.372	-

833

834

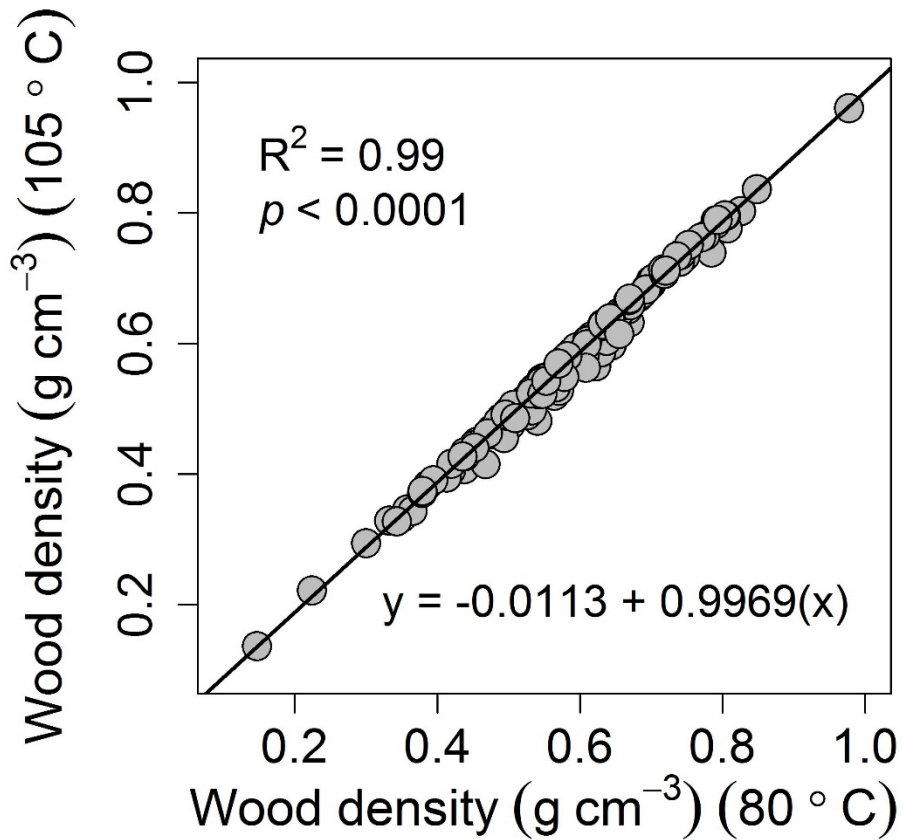
835 **Table S2.** Statistical moments of mean wood density (g cm^{-3}) distribution on species and stem levels for 41 permanent plots across the
 836 Andes-to-Amazon elevational gradient.

Plot	Elevation n (m)	Species WD								Stem-weighted WD							
		All arborescent life forms				Trees				All arborescent life forms				Trees			
		mean	sd	skewness	kurtosis	mean	sd	skewness	kurtosis	mean	sd	skewness	kurtosis	mean	sd	skewness	kurtosis
APK-01	3625	0.654	0.084	-0.415	-0.984	0.654	0.084	-0.415	-0.984	0.653	0.067	0.085	-1.355	0.653	0.067	0.085	-1.355
ACJ-01	3537	0.635	0.071	0.360	-0.250	0.635	0.071	0.360	-0.250	0.596	0.065	0.451	-0.862	0.596	0.065	0.451	-0.862
TRU-01	3450	0.589	0.115	-0.798	0.065	0.603	0.101	-0.835	0.756	0.600	0.069	-1.114	2.390	0.604	0.061	-0.676	1.195
TRU-02	3250	0.567	0.113	-0.480	-0.267	0.591	0.091	-0.340	0.507	0.600	0.103	-0.876	0.529	0.611	0.091	-0.878	1.211
TRU-03	3000	0.587	0.122	-0.618	-0.061	0.612	0.098	-0.529	1.002	0.650	0.088	-0.596	2.926	0.658	0.074	0.368	1.683
WAY-01	3000	0.589	0.107	-0.515	-0.022	0.602	0.093	-0.286	-0.015	0.628	0.066	-1.046	3.475	0.629	0.065	-0.944	3.229
ESP-01	2890	0.573	0.125	-0.424	-0.253	0.594	0.108	-0.444	0.621	0.614	0.089	-1.591	2.815	0.628	0.066	-1.238	3.756
TRU-04	2750	0.562	0.117	-0.576	-0.328	0.594	0.090	-0.607	1.382	0.561	0.130	-0.566	-0.969	0.618	0.078	-0.546	0.386
TRU-05	2500	0.558	0.146	0.220	-0.166	0.601	0.122	0.385	0.952	0.463	0.136	0.728	-0.772	0.586	0.098	0.056	0.195
TRU-06	2250	0.518	0.136	0.014	-0.787	0.559	0.120	-0.348	0.336	0.456	0.137	0.807	-0.768	0.556	0.124	-0.228	-0.699
TRU-07	2000	0.561	0.123	-0.401	-0.379	0.584	0.106	-0.492	0.619	0.564	0.139	-0.330	-1.128	0.623	0.096	-0.496	0.148
TRU-08	1800	0.562	0.123	0.105	-0.305	0.577	0.114	0.169	-0.040	0.547	0.143	0.189	-1.057	0.599	0.116	0.244	-1.014
SPD-01	1750	0.560	0.129	0.553	0.856	0.571	0.122	0.704	1.180	0.521	0.144	0.086	-0.398	0.569	0.115	0.255	0.775
CAL-01	1500	0.518	0.118	0.160	1.152	0.521	0.118	0.131	1.251	0.517	0.118	-0.359	0.854	0.517	0.118	-0.375	0.895
SAI-01	1500	0.552	0.119	0.335	0.950	0.559	0.115	0.410	1.160	0.553	0.119	0.448	0.111	0.559	0.117	0.472	0.143

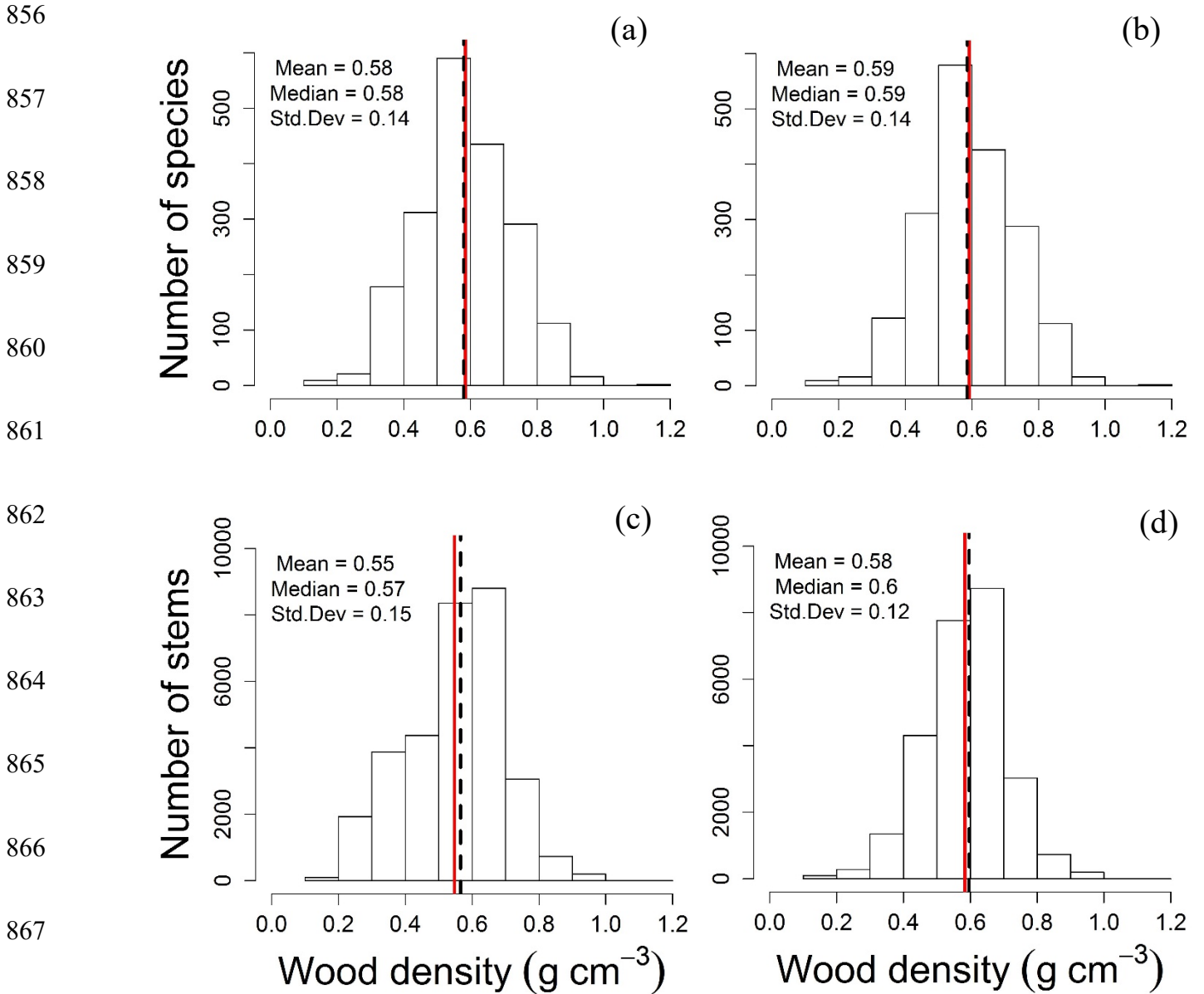
Plot	Elevatio n (m)	Species WD								Stem-weighted WD							
		All arborescent life forms				Trees				All arborescent life forms				Trees			
		mean	sd	skewness	kurtosis	mean	sd	skewness	kurtosis	mean	sd	skewness	kurtosis	mean	sd	skewness	kurtosis
SPD-02	1500	0.538	0.127	0.276	1.167	0.546	0.123	0.268	1.515	0.499	0.124	0.535	0.649	0.513	0.119	0.538	0.949
CAL-02	1250	0.534	0.140	0.415	1.792	0.536	0.138	0.461	1.889	0.545	0.111	-0.285	1.676	0.545	0.110	-0.271	1.686
SAI-02	1250	0.553	0.121	0.050	0.784	0.563	0.115	0.115	1.211	0.497	0.147	0.020	-0.217	0.555	0.112	0.354	1.289
TON-02	1000	0.549	0.132	0.464	0.258	0.558	0.126	0.606	0.283	0.529	0.118	0.514	0.523	0.534	0.115	0.605	0.563
PAN-03	850	0.616	0.140	0.057	-0.620	0.620	0.138	0.082	-0.610	0.622	0.150	0.310	-0.085	0.622	0.150	0.316	-0.075
TON-01	800	0.594	0.135	0.358	-0.037	0.601	0.131	0.402	0.051	0.586	0.134	0.591	0.472	0.589	0.132	0.621	0.543
PAN-02	595	0.606	0.148	0.371	0.005	0.608	0.146	0.429	-0.020	0.577	0.171	0.763	-0.053	0.577	0.171	0.770	-0.053
PAN-01	425	0.564	0.143	0.265	-0.226	0.570	0.138	0.381	-0.271	0.551	0.182	0.625	0.041	0.577	0.168	0.849	0.150
ALM-01	400	0.591	0.153	-0.349	-0.220	0.599	0.148	-0.355	-0.105	0.542	0.164	-0.232	-0.690	0.580	0.143	-0.329	-0.106
MNU-08	400	0.594	0.139	-0.114	-0.294	0.599	0.136	-0.116	-0.261	0.489	0.147	0.061	-0.438	0.550	0.120	0.274	0.079
BAB-01	387	0.574	0.151	-0.285	0.007	0.582	0.146	-0.280	0.181	0.521	0.168	-0.062	-0.650	0.563	0.149	-0.127	-0.168
MNU-04	358	0.587	0.145	-0.303	-0.290	0.593	0.140	-0.283	-0.253	0.541	0.150	-0.348	-0.545	0.580	0.128	-0.479	0.197
MNU-05	347	0.578	0.134	-0.237	-0.354	0.582	0.132	-0.232	-0.316	0.536	0.131	0.176	-0.230	0.551	0.128	0.208	-0.390
MNU-06	345	0.571	0.135	-0.045	-0.348	0.578	0.132	-0.042	-0.287	0.517	0.140	-0.086	-0.482	0.559	0.121	0.004	-0.355
MNU-03	312	0.582	0.144	-0.153	-0.274	0.588	0.142	-0.155	-0.232	0.518	0.149	-0.251	-0.579	0.552	0.131	-0.332	0.073
TAM-07	225	0.617	0.145	-0.281	-0.492	0.619	0.142	-0.205	-0.605	0.602	0.146	0.024	-0.893	0.602	0.145	0.069	-0.930
TAM-05	220	0.620	0.148	0.079	-0.319	0.623	0.145	0.145	-0.356	0.600	0.149	0.127	-0.604	0.606	0.144	0.227	-0.676
TAM-08	220	0.603	0.142	-0.054	-0.822	0.606	0.139	0.009	-0.889	0.583	0.151	-0.372	-0.287	0.614	0.123	-0.002	-0.261

Plot	Elevatio n (m)	Species WD								Stem-weighted WD							
		All arborescent life forms				Trees				All arborescent life forms				Trees			
		mean	sd	skewness	kurtosis	mean	sd	skewness	kurtosis	mean	sd	skewness	kurtosis	mean	sd	skewness	kurtosis
TAM-01	205	0.609	0.147	-0.152	-0.271	0.616	0.140	0.026	-0.474	0.504	0.187	0.008	-1.180	0.601	0.131	-0.111	-0.039
TAM-02	201	0.593	0.142	-0.110	-0.367	0.599	0.137	-0.010	-0.424	0.520	0.174	-0.147	-1.109	0.604	0.123	-0.346	0.112
TAM-06	200	0.581	0.143	-0.051	-0.171	0.591	0.138	-0.023	-0.102	0.484	0.175	-0.012	-1.072	0.574	0.125	-0.150	0.275
TAM-09	197	0.610	0.144	-0.088	-0.205	0.614	0.139	0.036	-0.315	0.567	0.167	-0.427	-0.530	0.619	0.122	-0.119	0.032
CUZ-01	190	0.558	0.164	-0.291	-0.007	0.567	0.160	-0.337	0.227	0.502	0.169	-0.378	-0.472	0.518	0.168	-0.594	-0.125
CUZ-02	190	0.571	0.143	-0.208	-0.162	0.579	0.137	-0.151	-0.076	0.529	0.149	-0.414	-0.542	0.585	0.105	-0.245	0.987
CUZ-03	190	0.588	0.151	-0.238	-0.243	0.595	0.147	-0.256	-0.081	0.551	0.150	-0.485	-0.249	0.593	0.118	-0.505	1.287
CUZ-04	190	0.585	0.137	-0.076	0.264	0.593	0.130	0.054	0.313	0.576	0.136	-0.027	-0.021	0.607	0.118	0.119	0.424

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852 **Fig. S1.** The effect of drying temperature on basic wood specific gravity (wood density) values is
853 shown by the relationship between wood density values dried at ~80 °C and 105 °C oven
854 temperatures (n = 145). The equation $y = -0.0113 + 0.9969(x)$ was used to calibrate all wood
855 density values obtained at the ~80 °C oven temperature.



870 **Fig. S2.** Overall wood density distribution along the Andes-to-Amazon elevational gradient for
 871 species including (a) all arborescent life forms and (b) tree species. Mean wood density for all
 872 stems (c) including all arborescent life forms and (d) tree stems. Solid red vertical lines indicate
 873 the means and dashed black lines indicate the medians.

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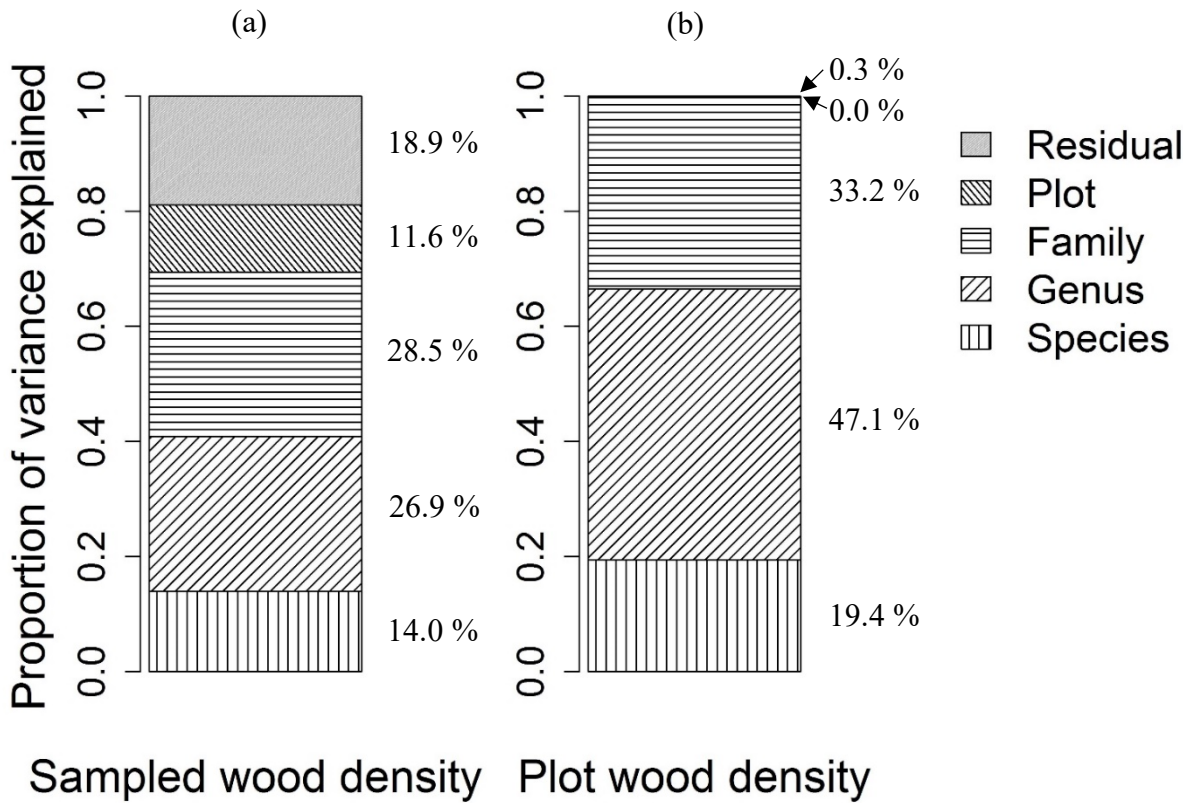
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889 **Fig. S3.** Variance partitioning of wood density across phylogenetic levels and environment (plot

890 level) for (a) field core-sampled and (b) plot level along the Andes-to-Amazon elevational

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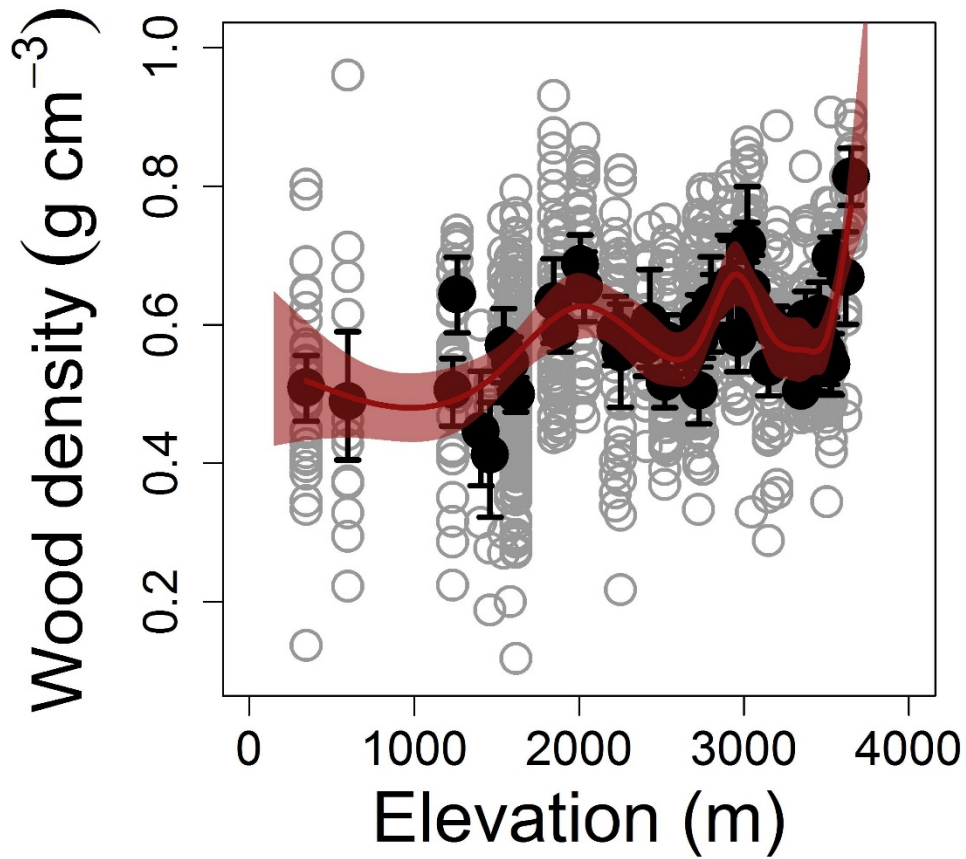
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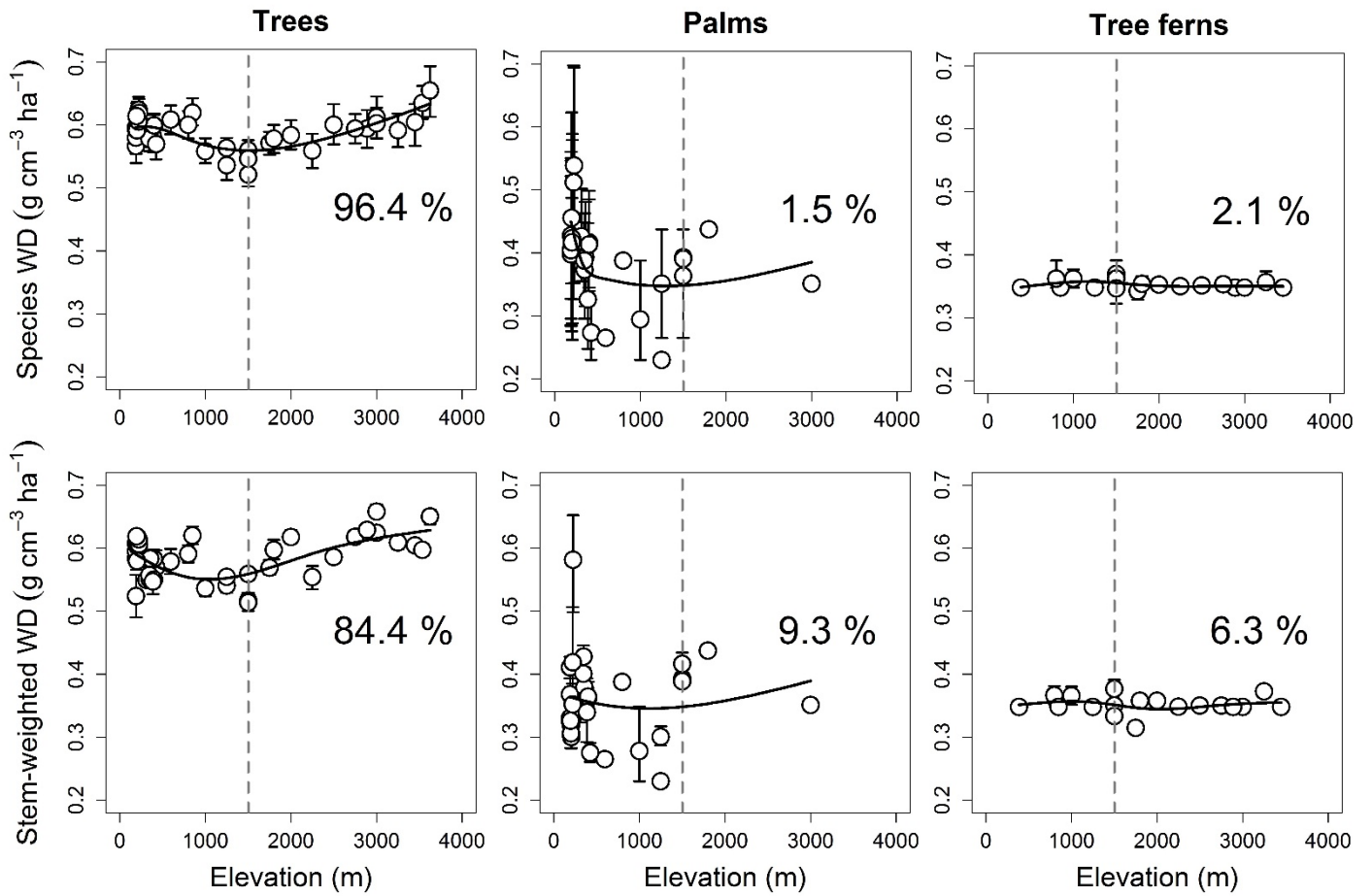
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Fig. S4. Sampled wood density along an Andes-to-Amazon elevational gradient. Gray open circles represent stem core samples across elevation ($n = 892$), and black solid circles represent the mean wood density among samples at each sampled site ($n = 51$). The red solid line is the generalized additive model (GAM) fit using a smoothing function with 95% confidence limits. Error bars depict bootstrapped 95% confidence intervals.



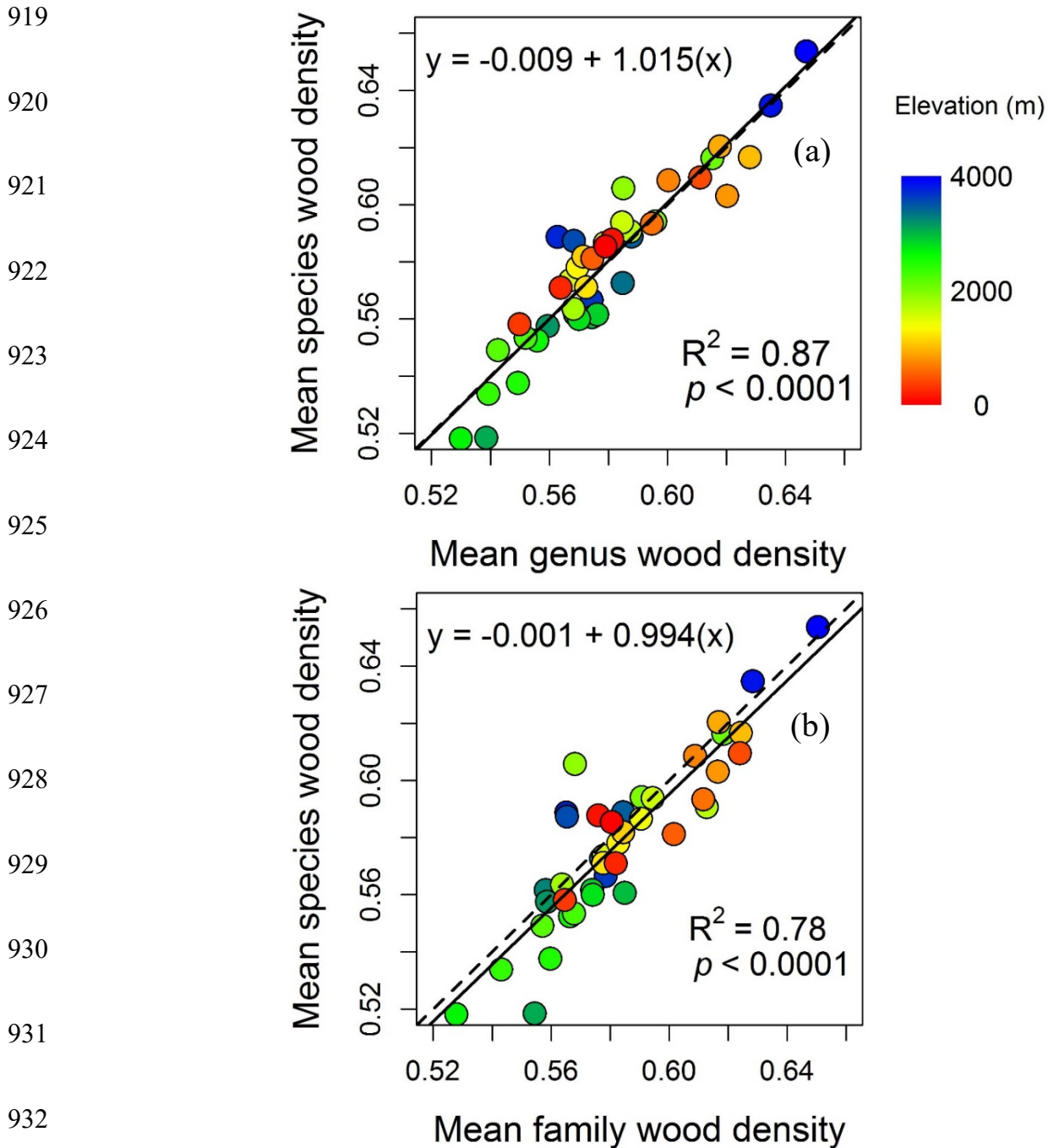
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914 **Fig. S5.** Plot-level mean wood density variation for trees, palms, and tree ferns along the Andes-
 915 to-Amazon elevational gradient. The upper panels represent the species' mean wood density, and
 916 the lower panels represent the stem-weighted wood density. Dashed vertical lines indicate the
 917 cloud base across the gradient. Percentages indicate the contribution of each life form to the
 918 overall wood density for species and Stem-weighted WD.



933 **Fig. S6.** Mean plot-level wood density for (a) genus and (b) family basis in function of species
 934 wood density. Solid lines represent best-fit linear regressions, dashed lines represent the 1:1
 935 relationship. Color ramp corresponds to plot elevations from the highest (blue) to the lowest
 936 (red) forest plots. The legend corresponds to the same forest plot colors for panels (a) and (b).