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RESEARCH ARTICLE

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

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Abstract

1. Understanding how functional traits are related to species diversity and ecosystem properties is a central goal of ecology. Wood density is a trait that integrates many aspects of plant form and function and is highly variable among species. Previous studies of wood density across elevational gradients have been based on limited sampling and have reported declines with increasing elevation, though even this simple pattern remains unknown, much less its underlying functional and evolutionary relationships.
2. Here, we use one of the longest and most speciose elevational gradients in the world, extending from the Andean tree line to the Amazon basin, to test the extent to which elevation, species composition, phylogenetic affinity and forest structure determine variation in wood density. Using field-collected wood samples and global databases, we assigned wood density to 1231 species and 31,330 stems across 41 (47.5 ha) mature forest plots arrayed across a 3500-m vertical gradient.
3. Our results show that mean wood density, either weighted by abundance, basal area or species, was highly variable but tended to decline from low to middle elevations and increase again from mid-elevations to the tree line. As a result of this non-linearity, forests at the Andean tree line had higher wood density than

their lowland Amazon counterparts. We observed an abrupt transition in wood density at the lower limit of persistent cloud formation (cloud base), where the lowest wood density values were found. The decline of wood density is attributed to a significant shift in life forms, with an abundance of tree ferns at middle elevations and a higher probability of landslides and disturbances favouring a suite of traits associated with low wood density, such as softer wood and higher elasticity. Species turnover explained most of the among-species variation across the gradient, with elevation having no consistent effect on within-species variation in wood density.

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

KEYWORDS

Amazon, Andes, elevational gradient, functional trait, species composition, wood density

1 | INTRODUCTION

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

1.1 | Interspecific and intraspecific wood density variability

Wood density is a functional trait that varies between species, within species and across individual ecological functions. Interspecific and intraspecific variation in wood density is closely related to diameter growth rate (King et al., 2005; Muller-Landau, 2004; Putz et al., 1983), hydraulic properties (Zanne et al., 2010) and other wood properties such as porosity, resistance and the number of vessel cells (Chave et al., 2009; Fortunel et al., 2014). At the community level, variation in wood density is often related to forest successional stage and life-history trade-offs between light-demanding and shade-tolerant species. Fast-growing and light-demanding species typically have lower wood density values than shade-tolerant species (Chave et al., 2009), though the variability in the relationship between the rate of growth and wood density is high and subject to multidimensional trade-offs (Rüger et al., 2012), with some fast-growing species having the highest wood density values recorded in tropical forests (e.g. *Tabebuia* spp.). The importance of within-species versus among-species variation in wood density is crucial for understanding its community-level significance and implications for ecosystem functioning. As tree communities change, they may exhibit functional redundancy in their responses. If intraspecific trends differ from interspecific trends, community responses will be influenced by species turnover and migration (Feeley et al., 2011; Rapp et al., 2012). Even less understood are the differences in wood density among life forms, for example, true trees (i.e. having secondary xylem) versus tissue densities of arborescent life forms without secondary xylem (e.g. palms and tree ferns). Varying abundances of these life forms are likely to affect ecosystem-level attributes such as carbon storage.

1.2 | Wood density variation across tropical environmental gradients

Existing studies of tropical forests across geographic and environmental gradients suggest high variation in wood density within and among tree communities (Fortunel et al., 2014; Williamson, 1984). For example, across the Amazon basin, wood density is higher in the central and eastern Amazon than in north-western Amazonia, both at the species level (Chave et al., 2006; Muller-Landau, 2004) and stand level per stem basis (Baker et al., 2004). This pattern can be explained by the disproportionate abundance and diversity of taxa with high wood density values associated with poor soils found in central and eastern Amazonia (Baker et al., 2004; Muller-Landau, 2004; ter Steege et al., 2006). However, there is still uncertainty about whether these patterns are caused by changes in wood density within all species in a community, or if they are influenced by the fact that tree communities are typically characterized by a few common species and many rare ones (Pitman et al., 2013; ter Steege et al., 2013). Patterns may be driven by hyperdominants or oligarchs—species that combine high local density with broad distributional ranges in Amazonia.

Of all the gradients in the Neotropics, the forested gradient from the tropical high Andes to Amazonian lowlands has the largest functional diversity and species richness and is likely the highest richness and plant functional diversity gradient on Earth (Asner et al., 2016). Although wood density is a key functional trait that links plant diversity with ecosystem function in tropical forests, our knowledge of this trait along environmental gradients in the Neotropics is incomplete, measured only at the lower end (0–2500 m) of an elevation gradient extending up to 4000 m and only at the species level (Chave et al., 2006). In addition, the observed trends of decreased productivity with elevation (Girardin et al., 2010) may be attributed to individuals of widely distributed species exhibiting higher wood density at higher elevations, a characteristic often associated with slower growth rates (Rapp et al., 2012). Species inhabiting higher elevations are likely to have greater wood density. We investigated the variation of wood density as a functional trait in an elevational gradient spanning ~3500 m from the Andean tree line to the Amazon basin on the eastern slope of the Peruvian Andes. To our knowledge, this is the first study in the Neotropics that assesses changes in wood density on an extensive elevational gradient using both field-collected wood samples and plot-based sampling approaches, including trees, palms and tree ferns. We ask (1) what is the pattern of intraspecific and interspecific variation in wood density across the Andes-to-Amazon gradient?; (2) what is the effect of elevation on community wood density variation and distribution, and how does this pattern differ when communities are defined by species composition and stem abundance? (3) what is the relationship between wood density and stem size across the elevation gradient? Understanding wood density helps clarify functional processes such as species adaptation to local conditions, tree growth strategies and the role of arborescent life forms in shaping forest structure and biomass estimates.

2 | METHODS

2.1 | Study site and climate

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

2.2 | Wood density calculation

We focused sampling on the dominant montane forest species because they are poorly or unrepresented in global databases. In our study area, we have registered 908 arborescent species above 1000 m elevation, and our field-taken wood samples comprise 34% of those species. We collected wood cores from 892 individuals representing 311 species of the dominant arborescent life forms—including trees, tree ferns (hereafter ferns) and palms from 2009 to 2015. We stratified sampling of wood cores across the gradient to ensure coverage of a broad range of taxa and to collect at least one individual for every species at each elevation. Core samples were collected in 51 sites ranging from 346 to 3650 m of elevation (Figure 1). An increment borer was used to extract wood core samples for trees and palms ≥10 cm diameter at breast height (DBH). The DBH of the sampled individuals ranged from 10 to 85 cm, and core samples were extracted from 1 to 1.3 m above the ground. For trees and palms, the wood cores were taken from the heartwood to the bark to capture density variation within the trunk. For arborescent ferns, sliced samples were taken from the trunk-like rhizomes in six different sections, and the average density value of the individual was used. Core samples were taken from individuals of targeted species outside of the permanent plots across the gradient (see below 'inventory plot data' section) to avoid effects on plants that are part of long-term studies.

All values here are reported as a *wood basic specific gravity*, which is defined as oven-dry mass divided by its green volume (Chave et al., 2006; Fearnside, 1997; Williamson & Wiemann, 2010) and henceforth called *wood density* in the text for simplicity. Wood density was calculated using the water displacement method with all samples oven-dried to constant mass and weighted to the nearest 0.001 g (Chave et al., 2006). Wood density values were first calculated at oven-dry temperature at ~80°C. Because of the

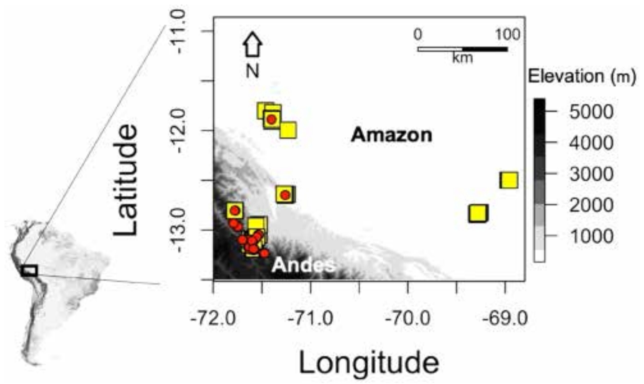

FIGURE 1 Location of the 51 wood collection sites (red circles) and the 41 permanent forest plots (yellow squares) on the eastern slope of the Peruvian Andes along an elevational gradient extending from the tree line at 3700 m to the Amazon basin at 190 m.

possible presence of bond water in the wood samples (Williamson & Wiemann, 2010), we used a subsample ($n = 145$) to calculate wood density at 105°C. We developed a correction equation (105°C WD = − 0.0113 + 0.9969 × 80°C WD; Figure S1) that was applied to calibrate the wood density values of the rest of the wood samples. We observed no significant difference among the wood density values at 105°C and 80°C (Mann–Whitney–Wilcoxon test, $n = 145$, $p = 0.31$). The overall mean difference between wood density values at 105°C and 80°C was 2.4% ± 0.38 (95% CI).

2.3 | Inventory plot data

Plot data were collected from 41 (47.5 ha) permanent mature forest plots across an elevation gradient ranging from 190 to 3625 m elevation, extending from lowlands through the montane forest up to the Andean tree line. A network of 24 1-ha permanent plots was established and monitored by the Andes Biodiversity and Ecosystem Research Group—ABERG, ranging from 387 to 3625 m elevation (ABERG PlotData, 2020). Additionally, 17 (23.5 ha) permanent plots were established by various investigators in lowland forests and are now monitored by the Amazon Forest Inventory Network—RAINFOR (Figure 1). The RAINFOR plot data were extracted from the ForestPlots.net database (ForestPlots.net et al., 2021). The permanent forest plots contain 31,330 stems greater or equal to 10 cm DBH and encompass 1950 species (of which 35% are morphospecies). Overall, the registered species in the transect belonged to 408 genera and 111 families (sensu APG IV).

2.4 | Botanical identification

All botanical vouchers taken with the wood core collections were identified and then compared and standardized with the permanent forest plot vouchers that were deposited in the Peruvian and US herbaria (CUZ, HUT, MOL, USM, and DAV, MO, F and WFU, respectively). Additionally, local flora and plant checklists were used as references (Farfan-Rios et al., 2015; Pennington et al., 2004; Vasquez & Rojas, 2016), and plant identifications were also confirmed by taxonomic experts. The APG IV classification (Chase et al., 2016) was followed for the taxonomy names, and the Taxonomic Name Resolution Service (TRNS) online application was used to standardize scientific plant names (Boyle et al., 2013).

2.5 | Data analysis

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

To analyse wood density variation across the elevational gradient at the plot level, we calculated an average species wood density value derived from the wood samples collected in the field (311 species, 892 individuals), and those values were assigned to each stem of a given species in the plot network across the transect. For stems with no measured density values from the transect, we incorporated wood density values from the Global Wood Density Data Base (Zanne et al., 2009). Overall, we compiled 1231 forest taxa from field-collected samples and published resources (Table S1). When density values were unavailable from the combined datasets of field-published resources at the species level, the mean values at the genus or family level were used. This was the case for the unidentified individuals to a species level (morphospecies) that accounted for 13% of the total individuals. The local plot-level mean value was used for the unknown taxa (0.8% of all taxa). We then calculated the mean wood density of each plot in two ways. First, we calculated the average wood density across all species present in each plot (species mean WD), and then, we calculated the mean wood density by weighting each species by its number of stems (stem-weighted WD). In addition, species mean WD was also weighed by basal area. We ran the analysis for all arborescent life forms (i.e. trees, ferns and palms) and for trees only, and in all the cases, we excluded lianas from the analysis. The outcome of this analysis indicates the influence of the arboreal life forms, the number and size of stems and the species composition turnover on plot-level wood density variation along the elevation gradient.

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

3 | RESULTS

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

3.1 | Interspecific and intraspecific variation of wood density along elevation

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

For the relationship of intraspecific variation in wood density with elevation, 83% of the species sampled ($n = 46$, ≥5 individuals) showed no relationship with elevation, and only eight species showed a significant response (Figure 2a). We found that the modal slope from the regressions was essentially zero ($n = 46$, $\bar{x} = 0.0003 \pm 0.0001$ [95% CI]), with a slight bias towards positive regression slopes (increasing intraspecific wood density with increasing elevation), as compared to negative slopes, with only eight slopes significantly different from zero (Figure 2a). However, we found large variation between tree species in both the sign and strength of the relationship. For example, wood density in *Clethra cuneata* shows a highly significant decrease with increasing elevation ($n = 45$, $F_{1,43} = 18.44$, adj. $R^2 = 0.28$, $p < 0.0001$; Figure 2b), whereas *Morella pubescens* ($n = 20$, $F_{1,18} = 2.90$, adj. $R^2 = 0.09$, $p = 0.11$; Figure 2c) and *Weinmannia bangii* ($n = 26$, $F_{1,24} = 0.0004$, adj. $R^2 = 0.00$, $p = 0.98$; Figure 2d) had no relationship with elevation. The wood density of *Alnus acuminata* ($n = 17$, $F_{1,15} = 7.75$, adj. $R^2 = 0.30$, $p = 0.013$; Figure 2e) and *Weinmannia fagaroides* both increased significantly with increasing elevation ($n = 28$, $F_{1,26} = 10.55$, adj. $R^2 = 0.26$, $p = 0.003$; Figure 2f).

3.2 | Plot-level wood density variation along the elevational gradient

Across the Andes-to-Amazon gradient, plot-to-plot mean wood density showed a nonlinear relationship with elevation (Figure 3; Table S1). Species mean WD for all arborescent life forms decreased slightly from 190 to 1500 m and remained constant from 1500 to 2500 m, subsequently increasing linearly up to the tree line at ~3650 m (Figure 3a). This trend was different when considering only tree species, with wood density decreasing from 190 to 1500 m and linearly increasing above cloud base up to the tree line; palms and fern species mean wood density did not show a relationship with elevation (Figure 3b; Figure S4). Stem-weighted WD for all arborescent life forms remained constant until 2000 m, declined abruptly between 2250 and 2500 m and then increased with elevation (Figure 3c). This trend changed for trees only, with stem-weighted WD slightly declining until the cloud base and then increasing up to the tree line (Figure 3d). Palm and fern stem-weighted WD were not related to elevation (Figure 3d; Figure S4). The influence of life forms on plot-level mean wood density variability was driven at middle elevations by arborescent ferns and by palms in lowland sites (Figure 3; Table S1). When mean species level wood density was weighted by basal area, weighted species mean WD for all arborescent life forms showed lower values and the stem-weighted WD for trees showed a stronger nonlinear relationship of wood density with elevation (Figure 4a,b), with the lowest values recorded in the submontane forest (Figure 4b). Species mean wood densities obtained using genus- and family-level identification were highly correlated with those using species-level data ($p < 0.0001$, $r = 0.94$; $p < 0.0001$, $r = 0.89$, respectively; Figure S5).

We observed that plot-to-plot wood density distributions and their statistical moments varied across elevation for both species and stem-weighted WD (Figure 5). The species WD skewness did not show a clear pattern from low to high elevations. However, the skew was more pronounced at the middle and low elevations for stem-weighted WD, indicating a clear influence of the abundance

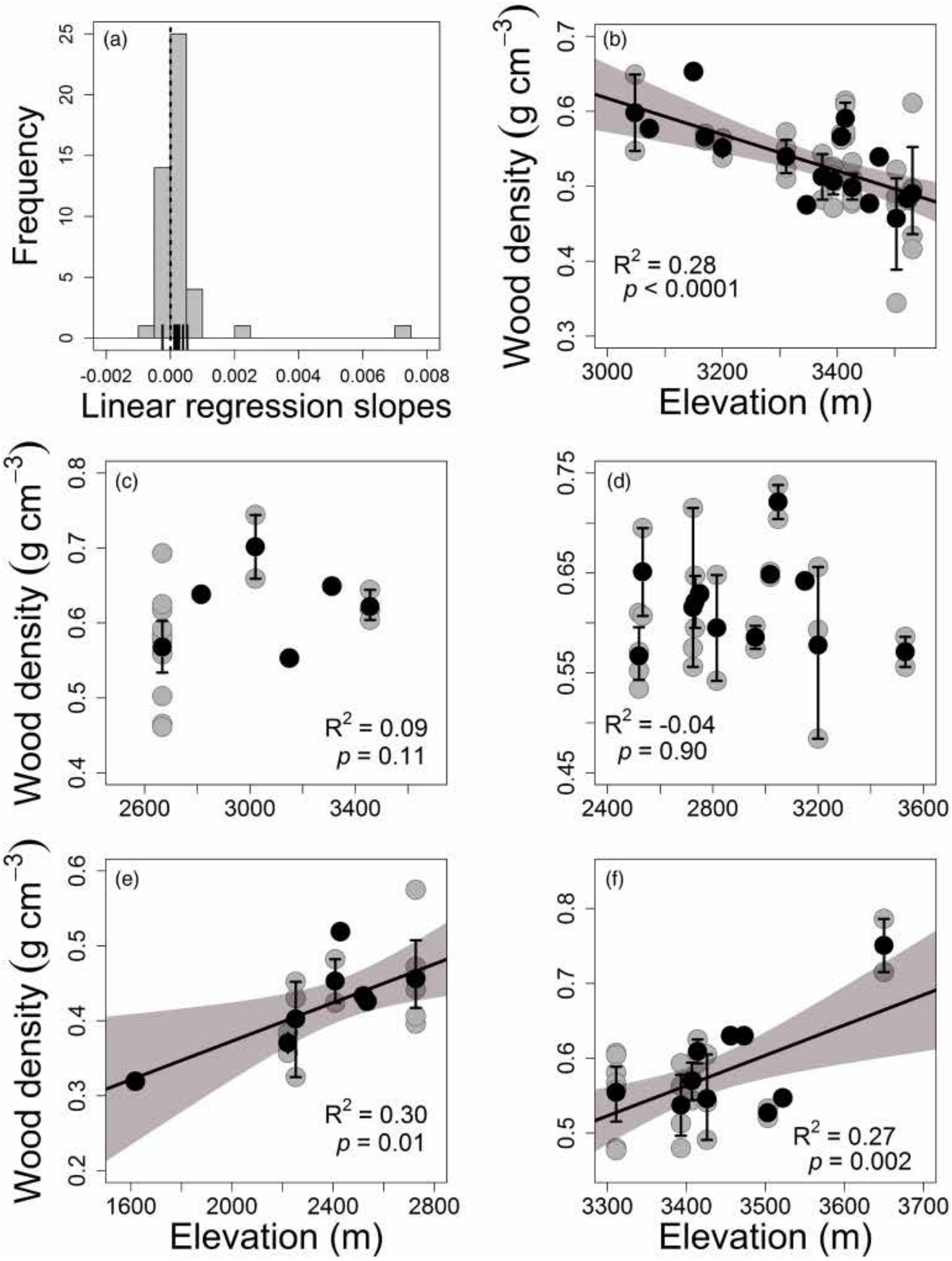

FIGURE 2 (a) Empirical distribution of within-species slopes of the linear regression between wood density and elevation ($n = 46$)—vertical bars represent the slopes significantly different from zero (8 positives and 1 negative). Intraspecific variation in wood density across elevations for (b) *Clethra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

of low wood density taxa (Figure 5; Table S2). Mean wood density differs significantly among forest types at the species and stem level (Figure 6a,b), but the difference for stem-weighted WD for all arborescent life forms was not significant among life zones along the gradient (Figure 6c,d; Kruskal–Wallis, $n = 7$; species WD for all arborescent life forms, $x^2 = 16.19$, $p = 0.013$; for trees, $x^2 = 15.35$, $p = 0.018$; stem-weighted WD for all arborescent life forms, $x^2 = 11.62$, $p = 0.071$; for trees, $x^2 = 15.67$, $p = 0.016$). For all taxa, species mean WD was lower at low elevations, reaching a minimum below cloud base in submontane forests and increasing through tree lines for all life forms and trees alone (Figure 6a,b). Stem-weighted WD remained constant towards the lower montane forest and increased only in the upper and tree line forests. When growth form was restricted to just trees, the pattern shifts, with a distinct drop

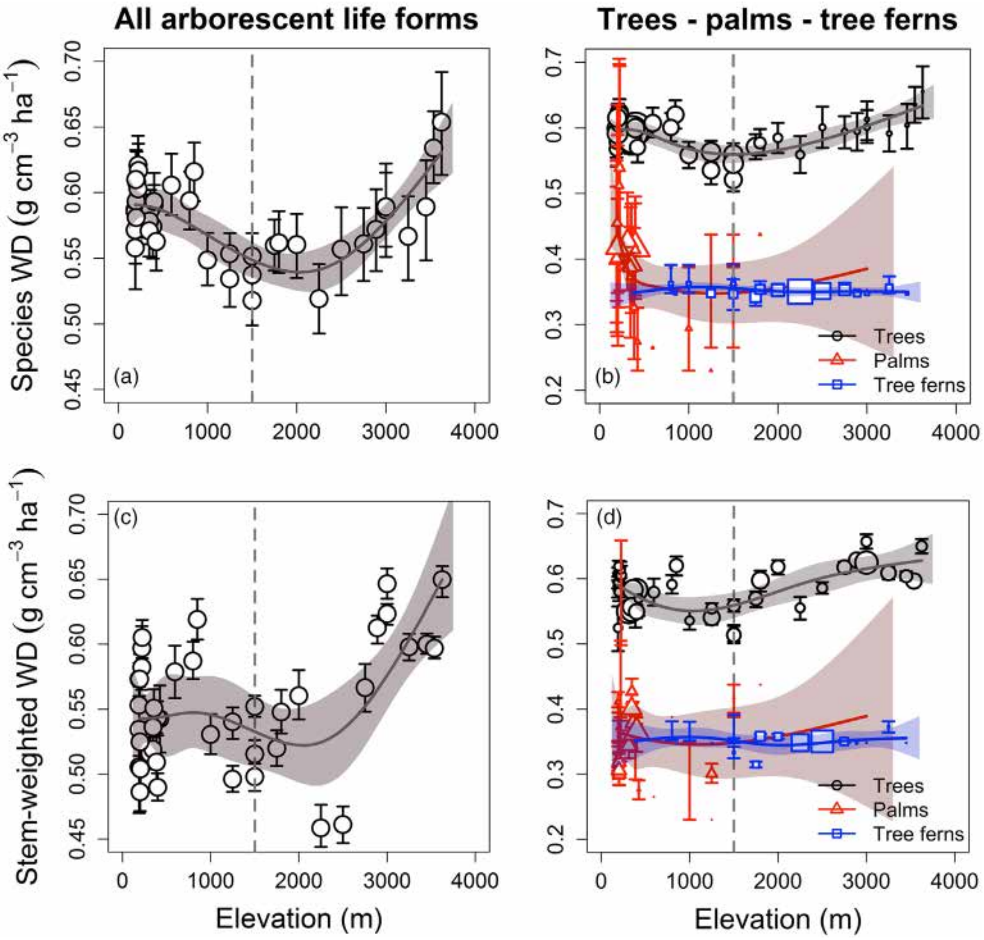

FIGURE 3 Plot-level mean wood density variation across 41 permanent forest plots along the Andes-to-Amazon elevational gradient for (a) species mean wood density for all arborescent life forms and (b) for trees, palms and fern species. (c) Stem-weighted mean wood density for all arborescent life forms and (d) for trees, palms and ferns. Symbol sizes for (b) and (d) are proportional to the number of species and abundance, respectively. Error bars depict bootstrapped 95% confidence intervals. Solid lines are generalized additive model (GAM) fit using a smoothing function with 95% confidence limits. Vertical dashed lines represent the approximate elevation of the cloud base.

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

3.3 | Wood density and forest structure

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

4 | DISCUSSION

Mean wood density changes substantially from lowlands to montane environments across the Andes-to-Amazon elevational gradient. Plot-level mean wood density showed a clear nonlinear relationship with elevation, and that pattern is explained by changes in species composition and species sorting based on local conditions rather than any general direct effect of elevation per se, with intraspecific variation in wood density being absent or showing no consistent trend with elevation. We observed that most of the wood density variation was a result of among-species differences and differences in the community composition because of changes in the relative abundances of different arborescent life forms rather than any within-species variability across the elevational gradient. Moreover, the abundance and distribution of arborescent ferns and palms had a large effect on mean wood density values along the gradient, decreasing wood density by 21% in montane forests dominated by tree ferns and 16% in lowland forests dominated by palms. When looking at community-level changes, the means and distributions of

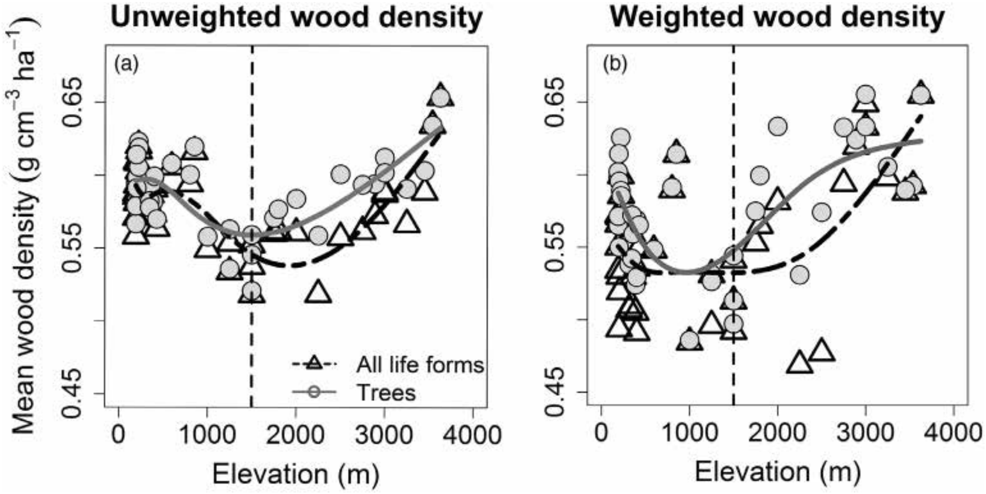

FIGURE 4 (a) Species mean wood density for all arborescent life forms and trees. (b) Species mean wood density for all arborescent life forms and trees weighted by basal area. Open triangles represent all arborescent life forms, and grey circles represent trees. Solid and dashed lines are generalized additive model (GAM) fit using a smoothing function. Vertical dashed lines represent the position of the cloud base along the gradient. Legend corresponds to the same life forms for (a) and (b).

wood density differed greatly depending on whether species were weighted equally or whether wood density values were weighted by individual (community-weighted mean density). To better understand community-level functional traits and their ecological importance, species lists from plots by themselves are not enough, and they need to be combined with the number of individuals and stem size (basal area).

4.1 | Nonlinear relationship of increasing wood density with elevation

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

The nonlinear relationship between wood density and elevation (Figure 3) is the result of species composition turnover and environmental filtering of life histories based on wood density or traits associated with wood density rather than a physiological response (intraspecific variation) to the elevation gradient, which is reflected in the decrease of the distributional variance with increasing elevation at species- and stem-weighted WD (Table S2). The variation in species mean WD resides predominantly at genus and family level, and that variation principally occurs between rather than within genera and families (Figure S3), indicating that wood density is highly conserved phylogenetically (Chave et al., 2006; Swenson & Enquist, 2007). The same phylogenetic pattern has been found for leaf mass per area measured from forest canopies across an Andean elevational gradient (Neyret et al., 2016), as well as a large suite of leaf functional traits (Asner, Anderson, et al., 2014), demonstrating that a wide range of plant functional traits is evolutionarily conserved. We know this is true for individual traits, but understanding the correlated suites of traits—the covariances among them—would give information about the major axes of variation or syndromes of functional traits if they do exist (Asner et al., 2016; Díaz et al., 2016). This is important in understanding the effects of environmental filtering and lineage sorting in shaping functional trait patterns across environmental gradients and raises questions about the relative influences of historical (e.g. Andean uplift) and ecological forces in shaping functional traits variation in tropical forests (Chave et al., 2006).

4.2 | Wood properties and the increase of wood density with elevation

Whereas wood density is taken as a comprehensive functional trait, wood has many functions and properties, and only some of them are correlated with density. For instance, non-lumen tissue, such as vessel walls, fibres and parenchyma, only explains 15% of the variation in wood density, and vessel lumen fraction is unrelated to wood density (Zanne et al., 2010)—what selective forces drive vessel and fibre trait variation remains unclear. Colder environments are potentially dominated by taxa that contain small vessels and tracheids that probably evolved before climate occupancy (Tyree & Zimmermann, 2002; Zanne et al., 2014). Forests at tree lines are exposed to air temperatures below 0°C and can reach ≤−5°C in the austral dry season (June), exposing plants to freezing conditions (Rapp & Silman, 2012). Thus, it is expected that these

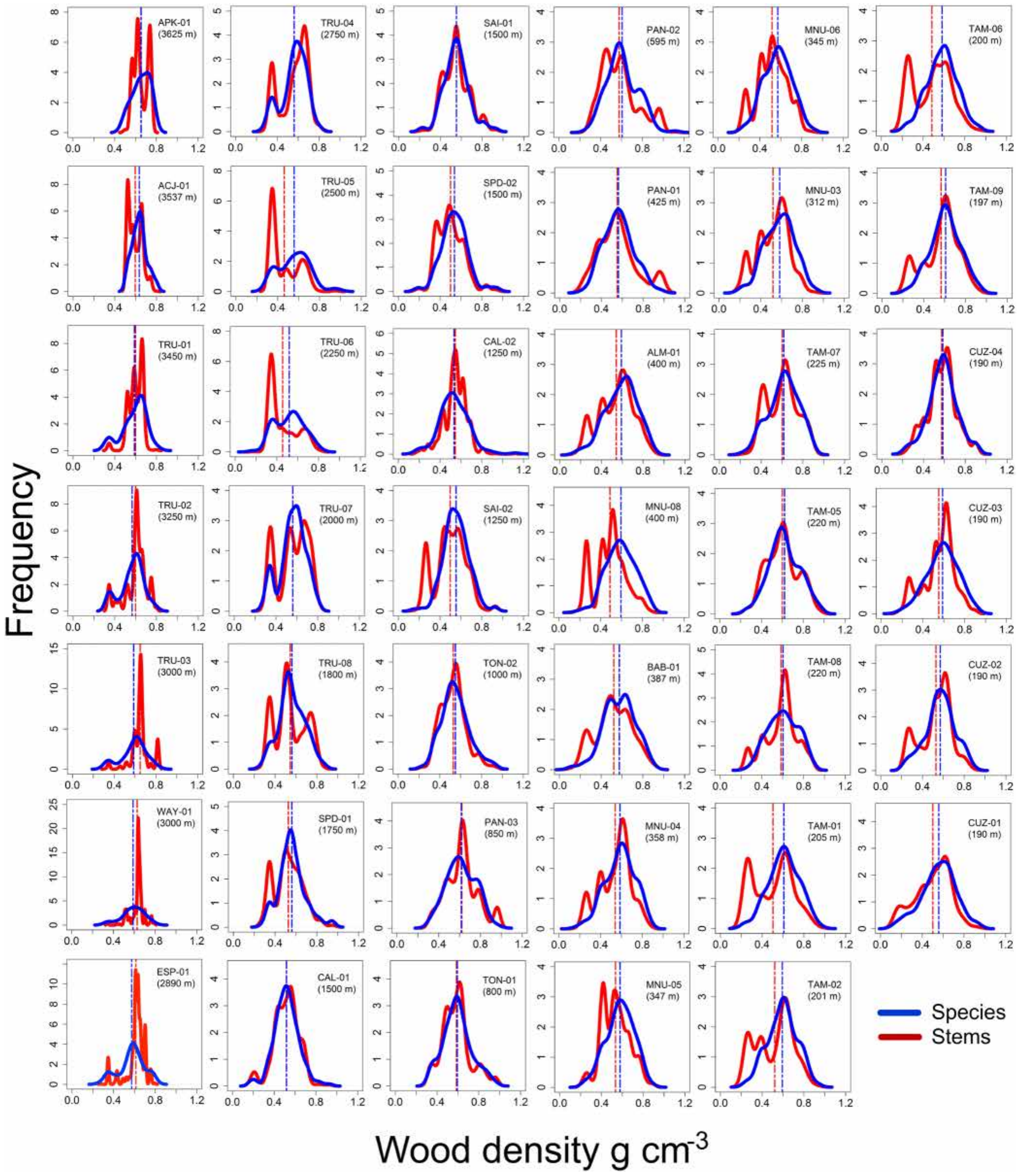

FIGURE 5 Wood density distributions for all species (blue lines) and all stems (red lines) across 41 forest plots along the Andes-to-Amazon elevational gradient. The data cover all arborescent life forms, including trees, palms, and tree ferns. Vertical dashed lines indicate the corresponding mean values for species or stems in each forest plot. Letters denote forest plot codes with their respective elevations. For detailed plot information, see Table S1.

taxa will contain numerous but short vessels with narrow diameters (Wheeler et al., 2007) and thick-walled fibres and vessels (Chave et al., 2009) explaining the high wood density values at higher elevations. In addition, wood density has shown an evolutionary correlation with other plant traits. For instance, wood density decreases with increasing leaf size but is generally unrelated to other

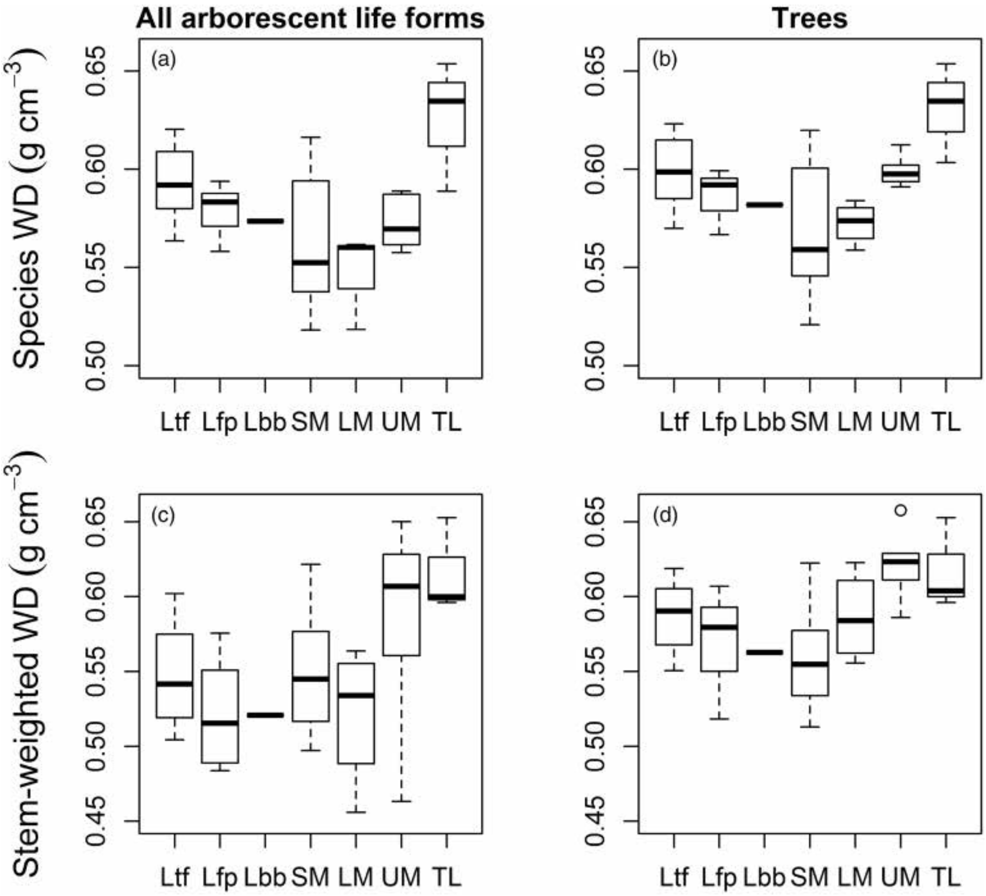

FIGURE 6 Plot-level wood density variation across forest types including: Lowland (Ltf = Lowland terra firme, Lfp = Lowland floodplain, Lbb = Lowland bamboo dominated forest; <500 m), submontane (SM: 500–1500 m), lower montane (LM: 1500–2500 m), upper montane (UP: 2500–3400 m) and tree line (TL: >3400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

functional traits such as seed size, fruit size and plant height (Wright et al., 2007). However, there are mixed findings for the wood density and leaf mass per area (LMA) relationship, showing either a positive relationship (Ishida et al., 2008) or none (Wright et al., 2007). Along a tropical elevational gradient, LMA increases linearly with increasing elevation (Asner et al., 2016), suggesting a positive relationship between wood density and LMA in the Manu-Tambopata elevational transect, although this remains untested. The complex relationships between wood and leaf function remain unclear but are important to understanding the leaf-wood construction costs in the plant growth spectrum between conservative and acquisitive species.

4.3 | Dominant taxa and life forms control wood density variation across the gradient

The role of dominant taxa and arborescent life forms impacts the observed patterns of stem-weighted WD variation across the gradient (Figures 3, 5 and 6). Trends of species and stem-weighted WD with elevation for all arborescent life forms were highly nonlinear (deviance explained = 57.5% for species and 36.4% for stem-weighted WD; Figure 3a,c; Figure S4), and this relationship is even stronger for stem-weighted WD when palms and ferns are excluded (deviance explained = 39.7%; Figure 3d; Figure S4). The nonlinear but positive relationship between wood density and elevation can be explained by the increase in the dominance of heavily wooded species at higher elevations (sensu Slik et al., 2010). More generally, forests at the tree line are dominated by taxa with higher wood density than their lowland counterparts, with lowest values at middle elevations (Figures 3, 5 and 6). For instance, the 10 most dominant species at our highest plot in the tree line (e.g. *Miconia alpina*, 0.740 g cm^{-3}) account for 17% of the total species but hold 70% of the total stems. This indicates that the highest values of stem-weighted WD at higher elevations (Figure 3c,d) are driven by a few dominant heavy-wooded species. Contrasting with the montane pattern, in the Amazonian floodplain forest, the 10 most dominant species (e.g. *Iriartea deltoidea* 0.265 g cm^{-3}), even though accounting for only 2% of the total species, they account for 38% of the total stems. If we exclude these dominant species, mean wood density values of the floodplain forests show a nonsignificant increase from 0.522 to 0.557 g cm^{-3} (Mann–Whitney–Wilcoxon test, $n = 6$, $p = 0.132$). This suggests that the abundance of these few species could explain the lower mean stem-weighted WD found in floodplains and,

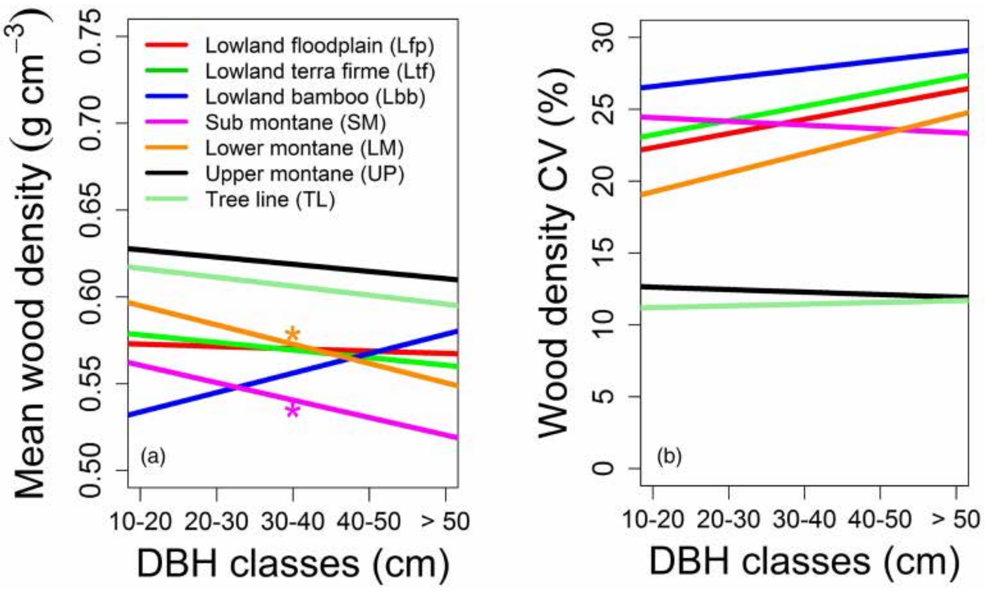

FIGURE 7 (a) Mean wood density variation for individual stems across DBH classes. Regression lines were computed using the mean averaged wood density across diameter classes for each forest type. Stars represent significant relationships. (b) Coefficient of variation (CV) of wood density across diameter classes–CV was calculated using the mean averaged wood density across diameter classes for each forest type. Colour lines correspond to the same forest types for both (a) and (b).

in general, in lowland forests. The plot-level variability in mean species and stem-weighted WD in the Amazonian forest (Figures 3 and 6) can also be associated with the difference in the geomorphology between the Holocene (floodplain) and Pleistocene (terra firme) sediments (Phillips et al., 2019).

Whereas general trends in mean wood density values were clear across the elevation gradient, there is substantial variability within any elevation, and much of this variation can be accounted for by the abundance of different arborescent life forms. Dicot trees were the dominant group along the gradient; however, arborescent ferns (i.e. Cyatheaceae and Dicksoniaceae) and palms (i.e. Arecaceae) had large effects on mean plot wood density variation in lower montane and lowland forests (Figures 3 and 5; Figure S4). For example, the abrupt decline of mean stem-weighted WD in the submontane and lower montane forests (Figures 3a,c, 5 and 6a,c) in the Manu-Tambopata elevational transect is explained by the high abundance of ferns (mean wood density 0.35 g cm^{-3}) at middle elevations. Excluding the dominance of arborescent ferns in the montane forest, mean stem-weighted WD significantly increases from 0.542 to 0.585 g cm^{-3} (Mann–Whitney–Wilcoxon test, $n = 13$, $p = 0.04$), but that difference is pronounced in some sites, for example in TRU-05 and TRU-06 plots, where arborescent ferns comprise 52% and 48% of the total stems at each plot, respectively, resulting in a 24% (for TRU-05) and 20% (for TRU-06) difference in stem-weighted WD as opposed to unweighted WD (Table S1). The same fern abundance patterns at the plot level were found at middle elevations in the Costa Rica elevational transect (Lieberman et al., 1996), indicating that the high abundance of this functional group has important effects on forest structure that translate to the carbon cycle in Neotropical montane forests.

4.4 | The lowest wood density and forest disturbance

Arborescent life forms have profound effects on the wood density variation across the elevation gradient, but this does not fully explain why wood density is lower in mid-montane forests near the cloud base. Excluding non-tree life forms, plot-to-plot wood density variation in true trees (those with secondary xylem) still follows the nonlinear relationship along the gradient (Figures 3 and 6; Figure S4). Forest dynamics in tropical mountains are highly influenced by natural disturbances with significant effects on the forest structure, diversity and function (Crausbay & Martin, 2016). Landslides and tree gaps may be the primary driving forces for vegetation turnover and changes in tree species composition in Andean tropical mountains. Accordingly, a plausible explanation for the consistent trends of lower values of mean wood density at middle elevations around the cloud base may be due to the effects of landslides. It has been shown that high landslide probability occurs at ~1500 m of elevation (Clark et al., 2015; Freund et al., 2021) just below and including the cloud base—below the cloud immersion zone—in the study area (Halladay et al., 2012). These are elevations with exceptionally high rainfall, with rain gauges at the site measuring 6–10.5 m year^{-1} of rain per year at 1400 m and 4–8.8 m year^{-1} of precipitation at 1800 m. The size, intensity and recurrence of landslides around the cloud base may lead to a high tree species turnover, facilitating the establishment of fast-growing species with low wood density (e.g. *Urera caracasana*, 0.180 g cm^{-3} and *Heliocarpus americanus*, 0.215 g cm^{-3}), resulting in highly dynamic and heterogeneous forests with high abundances of low wood-density species (Figure 8). Even large

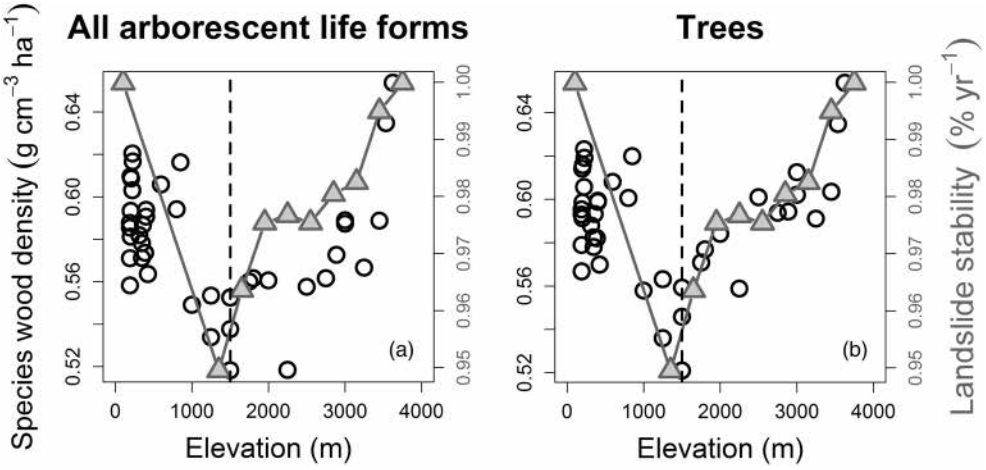

FIGURE 8 Mean wood density and landslide stability (LS) as a function of elevation along the Andes-to-Amazon transect. LS was calculated as the inverted scale of landslide probability (1 − landslide probability [%year^{-1}]) taken from Clark et al. (2015). Species mean wood density includes (a) all arborescent life forms and (b) trees only. Vertical dashed lines represent the cloud base in the gradient. Open circles represent mean species wood density and grey triangles represent landslide stability.

trees have significantly lower wood density values in the sub and lower montane forests than their lowland and upland counterparts (Figure 7). The light-woodedness may be due to the demands of establishing on high-turnover and competitive landscapes, but it also may be related to the exceptional quantity of precipitation and clouds and low VPD, making large vessel and light-woodedness possible, even for large trees. A way to differentiate between the hypotheses would be to look at the multivariate trait spectrum and see if other traits associated with regeneration on disturbed landscapes are higher at these elevations. In either case, the relationship between minimum mean community wood density with high landslide frequency may be important in understanding how tree communities are assembled.

4.5 | Ecosystem consequences

Wood density has been suggested to play a key role in understanding ecosystem properties, such as carbon cycling (Zanne et al., 2010), and is considered one of the six functional traits that bridge tree diversity and ecosystem function (Díaz et al., 2016). To improve above-ground carbon estimations in tropical forests, allometric equations now include wood density values to reduce uncertainties because it is critical to capture spatial patterns of carbon dynamics at local and regional scales (Malhi et al., 2006; Phillips et al., 2019). Here, we provide a wood density database to reduce uncertainties in carbon calculations, particularly for Andean montane forests where biomass declines with elevation (Asner, Knapp, et al., 2014; Malhi et al., 2016). Current above-ground biomass estimates across the Amazonian forests include palm communities in their calculations (Asner, Knapp, et al., 2014; Malhi et al., 2006). However, even though tree fern abundance exceeds 50% of stems per hectare in some elevations, they are not included in global tropical forest carbon estimates (Saatchi et al., 2011), excluding their contributions to tropical forest carbon stocks. This reinforces the importance of including all arborescent life forms in global forest biomass calculations.

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

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

AUTHOR CONTRIBUTIONS

William Farfan-Rios collected and analysed the data and drafted the manuscript. Miles R. Silman collected the data and drafted the manuscript. Sassan Saatchi, Imma Oliveras Menor, Yadvinder Malhi, Chelsea M. Robinson, Oliver L. Phillips, Alex Nina-Quispe, Juan A. Gibaja, Israel Cuba, Karina Garcia-Cabrera, Norma Salinas, John Terborgh, Nigel Pitman, Rodolfo Vasquez, Abel Monteagudo Mendoza, Percy Nunez Vargas and Fernando Cornejo collected the data. Craig A. Layman reviewed and edited the manuscript. All authors edited and approved the manuscript.

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CONFLICT OF INTEREST STATEMENT

We declare that there are no conflicts of interest.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.70100.

DATA AVAILABILITY STATEMENT

The Andes Biodiversity and Ecosystem Research Group (ABERG) is a team of researchers dedicated to understanding biodiversity, species distribution and ecosystem function in the Peruvian Andes. ABERG is committed to data exchange within the scientific community and promoting collaboration among other tropical ecosystem scientists. For more information and to request inventory forest plot data, contact Miles Silman (http://www.andesconservation.org/). The ABERG wood density dataset used in our study is available in the Zenodo digital repository https://doi.org/10.5281/zenodo.10864740 (Farfan-Rios et al., 2024). The Global Wood Density Data Base was extracted from the Dryad repository https://doi.org/10.5061/dryad.234 (Zanne et al., 2009). The RAINFOR forest plots data were extracted from the ForestPlots database https://forestplots.net/ (ForestPlots.net et al., 2021).

STATEMENT OF INCLUSION

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

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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

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

Figure S1: The effect of drying temperature on basic wood-specific gravity (wood density) values is shown by the relationship between wood density values dried at ~80°C and 105°C oven temperatures ($n = 145$).

Figure S2: Overall wood density distribution along the Andes-to-Amazon elevational gradient for species including (a) all arborescent life forms and (b) tree species.

Figure S3: Variance partitioning of wood density across phylogenetic levels and environment (elevation) for (a) field core-sampled and (b) plot level along the Andes-to-Amazon elevational gradient.

Figure S4: Plot-level mean wood density variation for trees, palms, and tree ferns along the Andes-to-Amazon elevational gradient.

Figure S5: Mean plot-level wood density for (a) genus and (b) family basis in function of species wood density.

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