# Variation in wood nutrients along a tropical soil fertility gradient

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## Summary

- Wood contains the majority of the nutrients in tropical trees, yet controls over wood nutrient concentrations and their function are poorly understood.
- We measured wood nutrient concentrations in 106 tree species in 10 forest plots spanning a regional fertility gradient in Panama. For a subset of species, we quantified foliar nutrients and wood density to test whether wood nutrients scale with foliar nutrients at the species level, or wood nutrient storage increases with wood density as predicted by the wood economics spectrum.
- Wood nutrient concentrations varied enormously among species from fourfold in nitrogen (N) to > 30-fold in calcium (Ca), potassium (K), magnesium (Mg) and phosphorus (P). Community-weighted mean wood nutrient concentrations correlated positively with soil Ca, K, Mg and P concentrations. Wood nutrients scaled positively with leaf nutrients, supporting the hypothesis that nutrient allocation is conserved across plant organs. Wood P was most sensitive to variation in soil nutrient availability, and significant radial declines in wood P indicated that tropical trees retranslocate P as sapwood transitions to heartwood. Wood P decreased with increasing wood density, suggesting that low wood P and dense wood are traits associated with tree species persistence on low fertility soils.
- Substantial variation among species and communities in wood nutrient concentrations suggests that allocation of nutrients to wood, especially P, influences species distributions and nutrient dynamics in tropical forests.

## Introduction

Tropical rainforests commonly occur on strongly weathered soils depleted in rock-derived nutrients such as calcium (Ca), potassium (K), magnesium (Mg) and phosphorus (P). As a consequence, productivity in tropical forests is assumed to be limited by the availability of one or more soil nutrients (Vitousek, 1984; Tanner *et al.*, 1998; Wright *et al.*, 2011). In addition to effects on productivity, spatial heterogeneity in soil nutrient availability can drive compositional variation in tropical tree communities at local scales and regional scales (John *et al.*, 2007; Baldeck *et al.*, 2013; Condit *et al.*, 2013). Differences among species in nutrient acquisition and allocation potentially underlie soil-based habitat partitioning in tropical forests (Chapin, 1980; Fine *et al.*, 2004; Palmiotto *et al.*, 2004; Baltzer *et al.*, 2005; Andersen *et al.*, 2012), and exacerbate plant–soil feedbacks that influence nutrient availability via nutrient deposition and mineralization from plant material (Wardle *et al.*, 2004). Consequently, quantifying variation in tree species allocation of limiting nutrients over soil fertility gradients is critical to understanding community assembly and biogeochemistry in tropical forests.

Tree nutrient-use strategies are most commonly evaluated through the nutrient stoichiometry of fresh leaves. Soil-based habitat distributions have been linked to foliar nutrient concentrations, because tropical plant taxa associated with high fertility soils contain greater concentrations of N and P in fresh leaves than species associated with low fertility soils (Tanner, 1977; Andersen *et al.*, 2012; Katabuchi *et al.*, 2012; Dalling *et al.*, 2016). Despite shifts in community mean foliar chemistry along soil fertility gradients (Vitousek *et al.*, 1988; Han *et al.*, 2005; Fyllas *et al.*, 2009; Ordoñez *et al.*, 2009; Hayes *et al.*, 2014), foliar nutrient concentrations are poorly constrained by soil nutrient availability in tropical forests, as variation in foliar nutrients among co-occurring species growing on the same soil habitat is nearly as great as regional variation in species foliar nutrients across soil fertility gradients (Townsend *et al.*, 2007; Fyllas *et al.*, 2009). Given the taxonomic control over foliar nutrient concentrations and the importance of tissue N and P concentrations in predicting rates of leaf (Santiago, 2007; Bakker *et al.*, 2011) and wood (Weedon *et al.*, 2009; Zanne *et al.*, 2015) decomposition, a trait-based approach leveraging taxon-specific chemical attributes has been advocated for modeling global carbon turnover from leaf (Cornwell *et al.*, 2008) and woody (Cornwell *et al.*, 2009) biomass. Although access to species-level information is rapidly expanding owing to the emergence of global trait databases (Kattge *et al.*, 2011), data on chemical attributes of wood are poorly represented in the literature (Chave *et al.*, 2009), despite wood containing roughly half of Ca, K, Mg,

N and P in live vegetation in tropical forests (Tanner, 1985; Wang *et al.*, 1991; Stanley & Montagnini, 1999; Bond, 2010). Trait inventories evaluating tropical tree species wood nutrient concentrations, in concert with more widely collected foliar and woody attributes, are necessary to more fully understand the variability among species in whole-tree nutrient use and the implications of this variability for ecosystem processes.

The extent to which foliar traits can be used to predict woody traits may depend on the range of soil habitats and taxonomic groups represented in the analysis. For instance, a global meta-analysis of 145 woody species found that stem and leaf nutrient concentrations were significantly, albeit weakly, correlated for both N ($r^2 = 0.20$) and P ($r^2 = 0.22$; Kerkhoff *et al.*, 2006). However, this pattern may be driven in part by latitudinal gradients in soil N and P availability, which are reflected in foliar nutrient concentrations (Reich & Oleksyn, 2004), rather than constraints across organs in nutrient allocation at the species level. Although decomposition rates of species wood, leaf and root tissues are correlated both within sites and across global scales (Freschet *et al.*, 2013), species wood and leaf decomposition rates are decoupled when angiosperm and gymnosperm taxa are analyzed separately (Pietsch *et al.*, 2014), suggesting that the allocation of nutrients and secondary metabolites might not be constrained across organs in co-occurring angiosperms. Furthermore, a multivariate analysis of wood and leaf characteristics in neotropical tree species found that physical wood and leaf traits load along orthogonal axes of variation (Baraloto *et al.*, 2010), indicating that the selection pressures that shape species tradeoffs among foliar traits might differ from those controlling the evolution of woody traits. Consequently, although we expect that species wood and leaf nutrient concentrations should be correlated at global scales, this relationship is not well understood in highly diverse tropical tree communities.

Wood and leaves differ in functional attributes that might disrupt a tight correlation between nutrient concentrations of these organs. Whereas woody biomass could provide a well-defended storage organ for nutrients, water and carbohydrates (Chapin *et al.*, 1990), leaves are a poorer storage organ due to their short lifespan and vulnerability to herbivores. Susceptibility to herbivory increases with foliar N concentration (Mooney & Gulmon, 1982; Andersen *et al.*, 2010), thereby creating a possible constraint on maximum investment of N in leaf metabolism, with consequences for other nutrients that are linked through stoichiometry. Compared to young, fully expanded leaves, stem nutrient concentrations display a greater relative increase in N and P concentrations in response to experimental N and P addition in seedlings in Panama (Schreeg *et al.*, 2014) and trees in China (Mo *et al.*, 2015), which may reflect a greater capacity for nutrient storage in wood compared with leaves. A global meta-analysis of 71 angiosperm species found not only that sapwood Ca, K, Mg, N and P concentrations all vary by an order of magnitude, but also, species vary considerably in their abilities to resorb nutrients as sapwood transitions to heartwood (Meerts, 2002). Given the potential variation in nutrient storage and remobilization in woody tissues among species, wood nutrients

may constitute an important dimension of functional variation in tropical tree communities.

The scarcity of interspecific wood nutrient data limits our understanding of co-variation between wood nutrients and other plant functional traits in tropical forests. This paucity of information was acknowledged in the development of the wood economics spectrum (WES; Chave *et al.*, 2009), a comprehensive meta-analysis emphasizing the inverse relationship between tree species wood density and mortality rates. The WES predicts tradeoffs among wood traits that facilitate fast growth (large conduit diameter) and adaptations that promote survival (high wood density, high storage capacity). In line with these predictions, stem nonstructural carbohydrate storage has been linked to increased wood density and decreased mortality rates in tropical forest saplings (Poorter & Kitajima, 2007). To date, studies evaluating the relationship between wood chemistry and the growth–survival axis have been limited to wood N and provide mixed evidence: wood N correlated positively with wood density and negatively with relative growth rate for 54 tree species in Panama (Martin *et al.*, 2014), whereas no relationship was found between the density and N content of wood in 23 tree species in Uganda (Becker *et al.*, 2012). Given that species leaf N concentration correlates negatively with wood density (Kraft *et al.*, 2008) and positively with species diameter growth rates in tropical forests (Poorter & Bongers, 2006), a positive relationship between wood nutrients and wood density would signal substantial functional decoupling among plant organs. To better understand how components of species nutrient use strategies relate to life history tradeoffs, wood nutrients must be evaluated with respect to foliar nutrients and wood density in co-occurring species in high-diversity tropical forests.

Here, we measured the concentrations of Ca, K, Mg, N and P in the wood of 106 Panamanian tree species growing in 10 montane and lowland forests spanning a range of soil 'available' nutrient concentrations comparable to the range observed throughout the tropics (Gartlan *et al.*, 1986; Baillie *et al.*, 1987; Phillips *et al.*, 2003; Quesada *et al.*, 2009). By exploiting this extreme soil gradient, we present the most robust examination to date of the natural variation in wood nutrient concentrations among species and sites in tropical forests. We hypothesized that if taxonomic variation in nutrient allocation influences the distribution of tree species across soil fertility gradients, then (1) community mean wood nutrient concentrations should correlate with soil nutrient availability, and (2) there should be substantial interspecific variation in wood nutrient concentrations within a site. We also evaluated whether wood nutrient concentrations in 58 montane forest species correlate with other species-specific functional traits, including foliar nutrients and wood density. If nutrient allocation to biomass is constrained across plant organs at the species level, then species wood nutrient concentrations should increase with species leaf nutrient concentrations, which are often negatively correlated with wood density. Alternatively, we hypothesized that if wood nutrient concentrations are proportional to the investment of nutrients into storage reserves, then tree species wood nutrient concentrations should correlate positively with wood

density, which is associated with persistence and survival strategies in tropical tree species.

## Materials and Methods

### Study site

We sampled foliar and woody tissue from six montane forest sites located within the Fortuna Forest Reserve (19 500 ha) and the adjacent Palo Seco Forest Protectorate (125 000 ha), henceforth Fortuna, in western Panama (Fig. 1a). This region encompasses old growth, lower montane forest, ranging between 700 and 1500 m above sea level (asl), with mean annual temperatures varying between 19 and 23°C (Cavelier *et al.*, 1997). There is strong interannual and spatial variability in precipitation among study sites, with annual rainfall ranging from 4000 to 9000 mm yr$^{-1}$. A distinct dry season occurs from January to April, but evapotranspiration does not exceed rainfall during this period (Cavelier *et al.*, 1997), with monthly rainfall accumulation exceeding 100 mm per month on average during the dry season in all but one site (Table 1).

Twelve permanent 1-ha forest plots were established at Fortuna in 2003 in which all trees > 5 cm diameter at breast height (DBH) are mapped, measured and identified to species. Plant tissue was sampled in six plots, chosen to maximize variation in soil nutrient availability across three geological substrates: rhyolitic tuff, andesite and porphyritic dacite (Andersen *et al.*, 2010). Soil pH ranges between 3.6 and 5.6 among sites, which coincides with substantial variability in Ca, K, Mg, N and P (Table 1). There is considerable floristic turnover among soil habitats, with only 22% of species shared between soils developed on dacite and rhyolite located < 15 km apart.

We sampled wood from four additional lowland sites in the Panama Canal watershed, part of a network of 1-ha plots established in the region by the Center for Tropical Forest Science (Fig. 1; Pyke *et al.*, 2001; Turner & Engelbrecht, 2011; Condit *et al.*, 2013). Two of the focal plots were located on peninsulas adjoining the Panama Canal (P13 and P25), and two plots in Soberanía National Park were located along Pipeline Road (P06) and Camino de Cruces (P24; plot codes from Pyke *et al.*, 2001). This region consists of semi-deciduous, seasonally moist forest, receiving *c.* 2500 mm of annual rainfall and with a mean annual
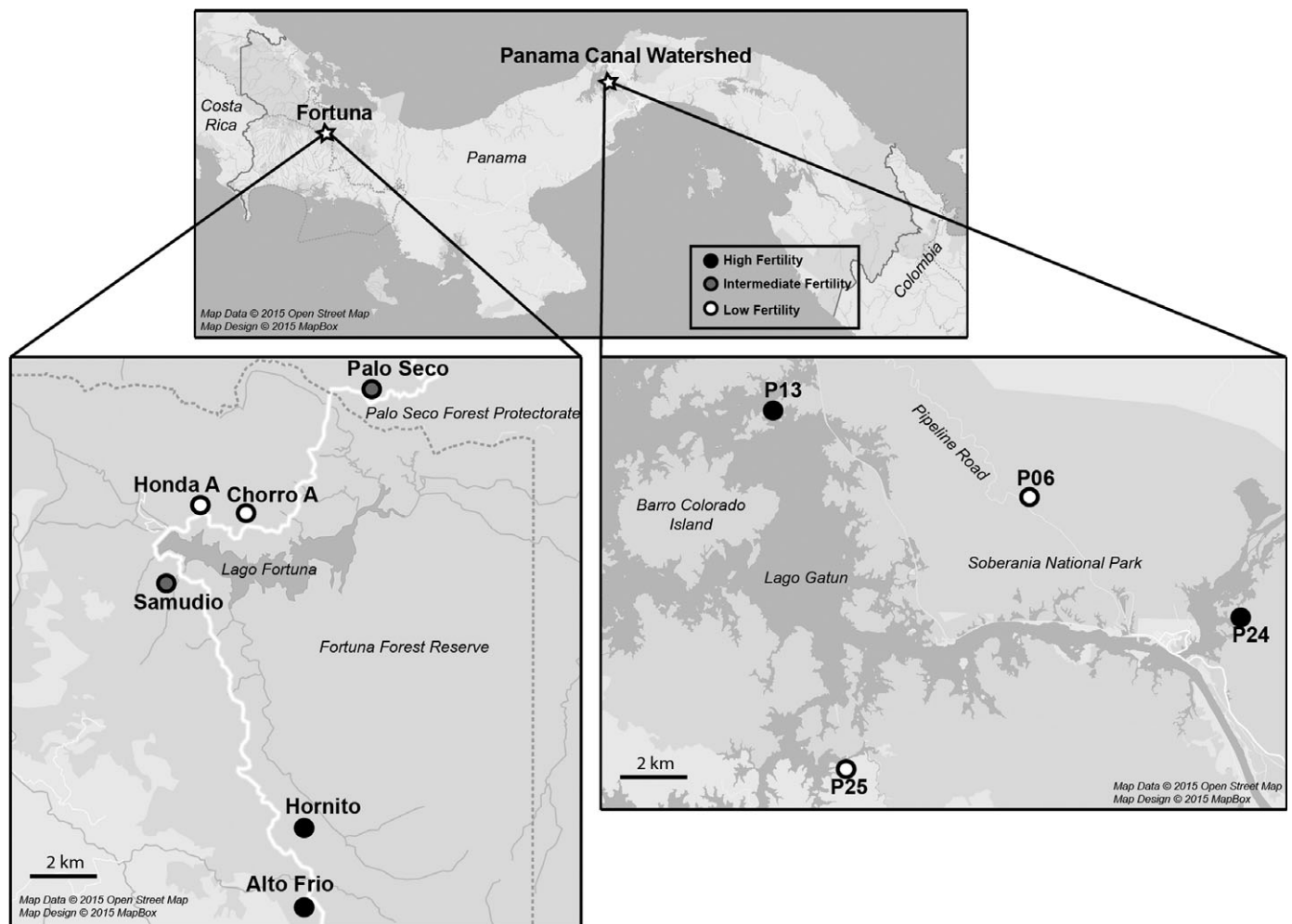


Fig. 1 Locations of 10 permanent 1-ha forest plots in Panama where we sampled wood. Leaves were also collected from the six Fortuna plots. Panama Canal Watershed sites are seasonally moist lowland forest located < 110 m above sea level (asl). Fortuna sites are wet lower montane forest located 800–1300 m asl. Plots are grouped by low, medium and high fertility based on soil chemical variables and geological parent material (see Table 1).

Table 1 Site location, environmental characteristics and species richness of 10 1-ha Panamanian forest plots near which wood core samples were collected

| Environmental variables | Montane forest: Fortuna | | | | | | Lowland forest: Panama Canal Watershed | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Chorro A | Honda A | Samudio | Palo Seco | Hornito | Alto Frio | P25 | P06 | P13 | P24 |
| [1]Protected area | Fortuna | Fortuna | Fortuna | Palo Seco | Fortuna | Fortuna | ACP | Soberanía | BCNM | Soberanía |
| Latitude (N) | 8°45′42″ | 8°43′3″ | 8°43′52″ | 8°46′43″ | 8°40′26″ | 8°39′15″ | 9°4′42″ | 9°9′23″ | 9°11′16″ | 9°7′25″ |
| Longitude (W) | 82°14′32″ | 82°14′22″ | 82°14′53″ | 82°11′53″ | 82°12′15″ | 82°12′54″ | 79°47′56″ | 79°44′39″ | 79°49′16″ | 79°40′36″ |
| Elevation (m asl) | 1100 | 1155 | 1215 | 878 | 1330 | 1100 | 110 | 30 | 55 | 50 |
| [2]Annual rainfall (mm yr$^{-1}$) | 5500 | 6200 | 4800 | 6200 | 5100 | 4600$^+$ | 2100 | 2300 | 2600 | 2200 |
| Dry season rainfall (mm per month) | 351 | 381 | 215 | 445 | 203 | 91 | 124 | 149 | 197 | 131 |
| [3]Soil properties | | | | | | | | | | |
| Geological substrate | Rhyolite | Rhyolite | Andesite | Andesite | Dacite | Dacite | Rhyolite | Marine Sediment (Gatuncillo) | Marine Sediment (Caimito) | Agglomerate |
| Bulk density (g cm$^{-3}$) | 0.13 | 0.29 | 0.39 | 0.41 | 0.25 | 0.66 | 0.87 | 1.05 | 0.67 | 0.59 |
| pH | 3.67 | 3.58 | 4.18 | 4.37 | 5.03 | 5.62 | 4.61 | 4.36 | 6.39 | 6.36 |
| Inorganic nitrogen (N; mg cm$^{-3}$) | 1.01 | 3.44 | 1.8 | 1.6 | 3 | 6.32 | 2.54 | 2.46 | 3.07 | 3.01 |
| Resin phosphorus (P; mg cm$^{-3}$) | 0.08 | 0.22 | 0.42 | 0.43 | 2.22 | 1.39 | 0.18 | 1.28 | 5.65 | 7.75 |
| Mehlich calcium (Ca; mg cm$^{-3}$) | 97 | 82 | 249 | 135 | 1358 | 3388 | 32 | 379 | 3706 | 1662 |
| Mehlich potassium (K; mg cm$^{-3}$) | 19 | 11 | 64 | 31 | 96 | 48 | 32 | 30 | 211 | 207 |
| Mehlich magnesium (Mg; mg cm$^{-3}$) | 19 | 20 | 53 | 40 | 254 | 551 | 67 | 117 | 737 | 539 |
| [4]Forest structure | | | | | | | | | | |
| Species richness | 72 | 135 | 125 | 167 | 139 | 83 | 84 | 78 | 60 | 60 |
| Basal area (m$^2$ ha$^{-1}$) | 32 | 44 | 35 | 32 | 55 | 43 | 20 | 19 | 25 | 31 |
| Stem density (stems ha$^{-1}$) | 1042 | 813 | 805 | 681 | 715 | 1050 | 302 | 484 | 429 | 355 |
| Species sampling | | | | | | | | | | |
| Species cored | 13 | 22 | 19 | 18 | 14 | 17 | 11 | 9 | 9 | 7 |
| BA represented by cored trees | 71% | 68% | 45% | 30% | 72% | 54% | 41% | 28% | 64% | 21% |

[1]Protected areas: Fortuna Forest Reserve (Fortuna), Palo Seco Forest Protectorate (Palo Seco), Panama Canal Authority (ACP), Soberanía National Park (Soberanía), and Barro Colorado Island Nature Monument (BCNM).
[2]Annual and dry season rainfall data at Alto Frio were collected from 2012 to 2014, all other Fortuna plots where monitored 2007–2014. Rainfall values from the lowland sites represent a multi-year averages.
[3]Bulk density, pH, inorganic N and Mehlich cations for Fortuna sites were published previously in Andersen et al. (2010).
[4]Forest structure for stems > 10 cm diameter at breast height (DBH) are from Pyke et al. (2001) for lowland sites and C. M. Prada & J. W. Dalling (unpublished), for montane sites.

temperature of 27°C (Pyke *et al.*, 2001). In the dry season, periods during which evapotranspiration exceeds rainfall are frequent and influence the recruitment of species in this area (Engelbrecht *et al.*, 2006). Focal plots are classified as mature secondary forest aged between 60 and 100 yr (Pyke *et al.*, 2001). Canal watershed plots were selected to maximize contrast along the soil fertility gradient (Table 1). The underlying geological substrates of the plots in order of increasing P availability are: rhyolitic tuff (P25), Gatuncillo Formation (marine sediment, P06), Caimito Formation (marine sediment, P13) and agglomerate (P24) (Turner & Engelbrecht, 2011).

### Plant tissue sampling and analysis

Wood core samples were extracted from 301 individual trees from 76 species at Fortuna and 104 trees from 30 species the Canal Watershed. In all plots, we sampled 7–22 woody species with the greatest basal area in each plot. We cored three trees > 10 cm DBH per species using a 4.3-mm Haglöf increment borer. Cores were taken at breast height (1.3 m) to a depth of half the DBH of the tree. Because coring canopy palms at Fortuna with hard exteriors and soft interiors damaged the borers, palms were not sampled in the Panama Canal Watershed. Consequently, compared to other sites, the sampled species represented a smaller proportion of plot basal area in P06 and P24 (Table 1) where the palm genera *Astrocaryum*, *Oenocarpus* and *Attalea* make up > 20% of the total basal area. Trees at Fortuna were cored outside permanent forest plots, but within 100 m of the plot boundary in February 2011. Lowland wood samples were collected from trees located within 1-ha plots in July 2013. At Fortuna, foliar tissue was collected for 58 of the species sampled for wood in July 2010. Three fully expanded shade leaves were collected with a pruning pole from three individuals per species. Although functional trait protocols recommend the collection of sun leaves for foliar nutrient analysis (Cornelissen *et al.*, 2003), we sampled shade leaves to maximize the number of species included in our study, because 43% of tree species with individuals > 10 cm DBH in the Fortuna plots do not reach the canopy (DBH > 30 cm). Analysis of foliar plasticity to light in 38 tropical tree species found that rank order in species mean N and P concentrations is preserved across sun and shade leaves (Rozendaal *et al.*, 2006), indicating that the choice of sun vs shade leaves should should not affect how wood and leaf nutrients co-vary across species. Wood and leaf samples were stored on ice until processing. Each wood core was divided into segments ≤ 5 cm and volume determined by Archimedes' principle. Segments were then dried to constant mass at 60°C and wood density was calculated as segment dry mass/fresh volume.

All leaf material collected for each tree, including petioles and rachii, were ground together in a KLECO Tissue Pulverizer (Kinetic Laboratory Equipment, Visalia, CA, USA). A mini-Wiley Mill (Thomas Scientific, Swedesboro, NJ, USA) was used to grind wood core samples in 5 cm segments to account for possible radial differences in wood attributes (Lachenbruch *et al.*, 2011). We used 5 cm as a critical threshold of change in wood chemistry based on the steep observed decline in nonstructural carbohydrate concentrations between 4.5 and 6 cm in wood cores taken from lowland Panamanian tree species (Würth *et al.*, 2005). We were unable to categorize segments visually as heartwood or sapwood because the heartwood/sapwood transition is often gradual in tropical trees (Jordan & Kline, 1977). Nitrogen concentrations in leaf and wood tissues were tested on a Costech Elemental Analyzer (Valencia, CA, USA) for samples analyzed in Illinois and a Thermo Flash 1112 Elemental Analyzer (Waltham, MA, USA) for samples analyzed in Panama. A subset of samples tested on both Elemental Analyzers also closely and linearly correlated ($r^2 = 0.92$, $n = 10$), although a correction factor of $-0.18$ was applied to all samples tested in Panama to ensure consistency in the two datasets. To prepare wood and leaf material for Ca K, Mg and P analysis, samples were dry ashed at 550°C for 1 h and the ash dissolved in 1 M $HNO_3$ (Karla, 1998). Base cations for all samples and P in tissues collected at Fortuna were measured using inductively coupled plasma-optical emission spectrometry (ICP-OES) on an Optima 2000 DV (Perkin Elmer, Waltham, MA, USA). A subset of Fortuna wood samples with P concentrations below the ICP-OES detection limit and all lowland wood samples were analyzed for P via automated molybdate colorimetry using the Lachat Quickchem 8500 (Hach Ltd, Loveland, CO, USA). For samples above the detection limit of the ICP analyzed on both instruments, P measurements by spectrometry and colorimetry were closely correlated ($r^2 = 0.95$, $n = 10$) with an intercept that did not differ significantly from zero. We included certified reference samples (NIST 1515, apple leaves) and internal laboratory control standards in all analyses.

### Soil sampling and analysis

Soil cores were taken to a depth of 10 cm from 13 locations in each 1-ha plot during the wet season at both lowland and montane sites. Bulk density was determined by drying a known volume of soil at 105°C. Soil pH was determined in a 1 : 2 soil to deionized water ratio using a glass electrode. Total soil inorganic N was calculated as the sum of soil nitrate and ammonium measured in 0.5 M $K_2SO_4$ extracts and determined by automated colorimetry on a Lachat Quikchem 8500 (Hach Ltd). Readily exchangeable P, which approximates plant available P, hereafter 'resin P', was determined by extraction with anion-exchange membranes (Turner & Romero, 2009). Base cations were extracted in Mehlich-3 solution (Mehlich, 1984) with detection by ICP–OES on an Optima 7300 DV spectrometer (Perkin-Elmer).

### Statistical methods

**Response of site-mean wood chemistry to soil nutrient availability** For consistency, we limited our analyses of plot and interspecific variation in wood nutrient concentrations and densities to data from the outer 5 cm of wood because the majority of trees cored were not big enough to yield multiple 5 cm segments. The community weighted mean (CWM) nutrient concentration for each 1-ha plot was calculated as the average of species mean wood nutrient concentrations (in the outer 5-cm annulus)

weighted by basal area of each species sampled in the 1-ha plot (trees > 10 cm DBH). Ordinary least squares (OLS) regression was used to fit the relationship between CWM wood and plot mean soil nutrient concentrations, and between species mean wood nutrient concentrations and respective plot level soil nutrient concentrations to determine how much variation in species wood nutrient concentrations is explained by soil nutrients alone. Wood nutrient concentrations and soil variables were log-transformed before regression analyses to meet the assumption of normality of errors.

**Wood vs leaf scaling relationships**  We modeled the relationship between species mean wood and leaf nutrients among organs for 58 woody species sampled for both leaf and wood nutrients at Fortuna. If a species was sampled in more than one plot, we used the mean species value across all plots so that there were no duplicate species in the analysis. We modeled wood-leaf scaling as a power function ($Y \sim aX^b$), which was transformed to be evaluated as a linear relationship ($\log(Y) \sim b \times \log(X) + \log(a)$). If the exponent or slope of this relationship ($b$) differs from one, then scaling is nonlinear, indicating that the nutrient concentration of one tissue is more constrained in one tissue vs the other. We fitted the log–log relationship between species mean leaf and wood values for each element using type II Major Axis (MA) regression in the *lmodel2* package in R (Legendre, 2011). MA regression is recommended over OLS regression in this case because there is similar measurement error in both variables. We used 95% confidence intervals to determine if $b$ differed significantly from 1. Because we modeled mean wood nutrient concentrations as a function of leaf nutrient concentrations, $b > 1$ indicates that leaf nutrients are more constrained among species than wood nutrients. We determined $r^2$ values from OLS regression of each relationship to find the proportion of variance in species mean wood nutrient concentrations explained by foliar nutrient concentrations.

Because some species are more closely related in evolutionary history than others, species trait values may be considered nonindependent and therefore violate the assumption of linear regression. To determine if species wood and leaf nutrient concentrations co-vary after accounting for evolutionary history, we tested relationships for the phylogenetically independent contrasts (PICs) of log-transformed species mean wood and leaf nutrient concentrations (Felsenstein, 1985). We constructed a phylogenetic tree for the species in our study from the Angiosperm Phylogeny Group super tree (APG III; http://www.mobot.org/MOBOT/research/APweb) using Phylomatic v3.0 (Webb & Donoghue, 2005). We used the fossil-derived ages of tree taxa listed in Wikstrom (Wikström *et al.*, 2001) to determine the branch lengths of this tree using BLADJ in Phylocom (Webb *et al.*, 2008). Because the APG III tree is resolved to the family level for most lineages, genera were drawn as polytomies nested within families and species were drawn as polytomies within genera. Before phylogenetic analyses, polytomies in the tree were broken randomly. PICs for the log of each species trait value were calculated using the *ape* package (Paradis *et al.*, 2004) in R. We used MA regression to fit the scaling relationship between

the PICs of wood and leaf nutrient concentrations. PIC models were fitted through the origin as suggested in Garland *et al.* (1992).

**Wood nutrient concentrations vs wood density**  For 76 woody species cored at Fortuna, we tested if species mean wood nutrient concentrations co-vary with each other and with woody density using MA regression. We log-transformed wood nutrient concentrations before regression analysis to meet the assumption of normality of errors. We performed the same regression analysis for the PICs of log-transformed species mean wood nutrients and nonlog-transformed wood density. The significance threshold of regression tests was adjusted using the Bonferroni correction to account for multiple comparisons. If a species was cored in > 1 plot, we used the average species mean across all plots so that there were no duplicate species in the analysis.

**Radial variation in wood nutrient concentrations**  For the 110 trees, we fitted the log–log relationship between the nutrient concentrations of the inner (5–10 cm in depth) vs outer (0–5 cm in depth) wood annuli for each element using MA regression. We used 95% confidence intervals to determine if the intercept differed from zero and the slope differed from 1. We also calculated the coefficient of determination $r^2$ from OLS regression to evaluate how well the concentration of inner annuli can be predicted from outer annuli.

We evaluated if species vary in radial patterns of wood nutrient allocation for 18 species for which we had available data on both inner and outer wood segments for $\geq 3$ individuals per species. For each tree, we calculated the percentage radial discrepancy in wood nutrients as: (outer − inner)/outer × 100. We determined the mean radial discrepancy for each species $\pm 1$ SE to determine if the change in wood nutrient concentrations from the outermost segment to adjacent inner segment is < 0, = 0, > 0.

## Results

### Interspecific and inter-site variation in wood nutrients

Of the elements measured in the outer 5 cm of wood across the 106 tree species sampled in this study, mean concentrations of N were greatest ($2557 \pm 70 \, \mu g \; g^{-1}$), followed by Ca ($2082 \pm 160 \, \mu g \; g^{-1}$), K ($1622 \pm 80 \, \mu g \; g^{-1}$), Mg ($492 \pm 40 \, \mu g \; g^{-1}$) and P ($111 \pm 7 \, \mu g \; g^{-1}$; Table 2; Supporting Information Table S1). Although wood nutrient concentrations varied considerably among species and sites, the magnitude of this variability was not consistent among elements (Table 2). The range in mean wood N among species (fivefold) was less than the smallest range of species means measured for rock-derived elements including P (35-fold), K (36-fold), Ca (47-fold) and Mg (51-fold). When species averages were weighted by basal area to calculate CWM nutrient concentrations, there was also a greater range of values among sites in wood P and cations compared to wood N (Table 2): N (1.8-fold), Mg (2.5-fold), K (4.5-fold), Ca (7-fold) and P (8.5-fold).

## Wood nutrient concentrations vs soil nutrient availability

In line with our predictions, CWM wood nutrient concentrations (a plot-level estimate of wood nutrient status) for Ca, K, Mg and P were significantly correlated with the plot mean nutrient concentrations in the topsoil (Fig. 2a–c,e). CWM wood P concentration correlated most strongly with its respective soil metric ($r^2 = 0.71$), followed by Mg ($r^2 = 0.64$), K ($r^2 = 0.58$) and Ca ($r^2 = 0.49$). Although CWM wood N was not significantly correlated with soil inorganic N ($r^2 = 0.00$, $P = 0.519$; Fig. 2e), soil resin P was a strong predictor of CWM wood N ($r^2 = 0.59$, $P = 0.009$), indicating that CWM wood N concentrations varies along the fertility gradient.

When species-level wood nutrient means were modeled as a function of plot-level soil nutrient concentrations (Fig. 2f–j;

Table S2), the relationship between wood Mg and soil Mg was no longer significant ($r^2 = 0.01$, $P = 0.141$). For all nutrients, the slope of the species means wood vs soil regression was smaller in magnitude than the slope of the CWM (basal-area weighted) wood vs soil regression fit (Fig. 2; Table S2), suggesting that species with high basal area better reflect local soil nutrient availability than rare or small stature species.

## Wood vs leaf nutrient concentrations

For 58 montane tree species for which we analyzed both wood and leaf nutrient concentrations, species mean leaf and wood nutrient concentrations were significantly positively correlated for all elements evaluated, supporting the hypothesis that nutrient allocation is constrained across organs at the species level. Among significant relationships, wood and leaf tissue chemistry was most strongly correlated for P ($r^2 = 0.36$; Fig. 3e) and most weakly correlated for Mg ($r^2 = 0.18$; Fig. 3c). For Ca, K, Mg and P, the slope of the wood vs leaf relationship ($b$) was significantly > 1, indicating that wood nutrient concentrations scale nonlinearly with leaf nutrient concentrations (Table 3; Fig. 3). By contrast, the slope of the leaf vs wood regression did not differ from 1 for N (Table S2; Fig. 3d), indicating that N scales isometrically between wood and leaf tissues.

When wood and leaf nutrient concentrations were corrected for evolutionary history using PICs, the scaling relationship remained significant for all nutrients but Mg (Table 3). Slopes of PIC models did not differ from observed models for any nutrient (Table 3). Scaling exponents of relationship between wood–leaf PICs remained significantly > 1 for K and P, and the $b$ value of the wood–leaf PIC for Ca marginally overlapped with 1 (95% CI = 0.99–2.10).

**Table 2** Summary statistics of community-weighted mean (CWM) and species mean wood nutrient concentrations for 106 tree species sampled across six lowland and four montane forest plots

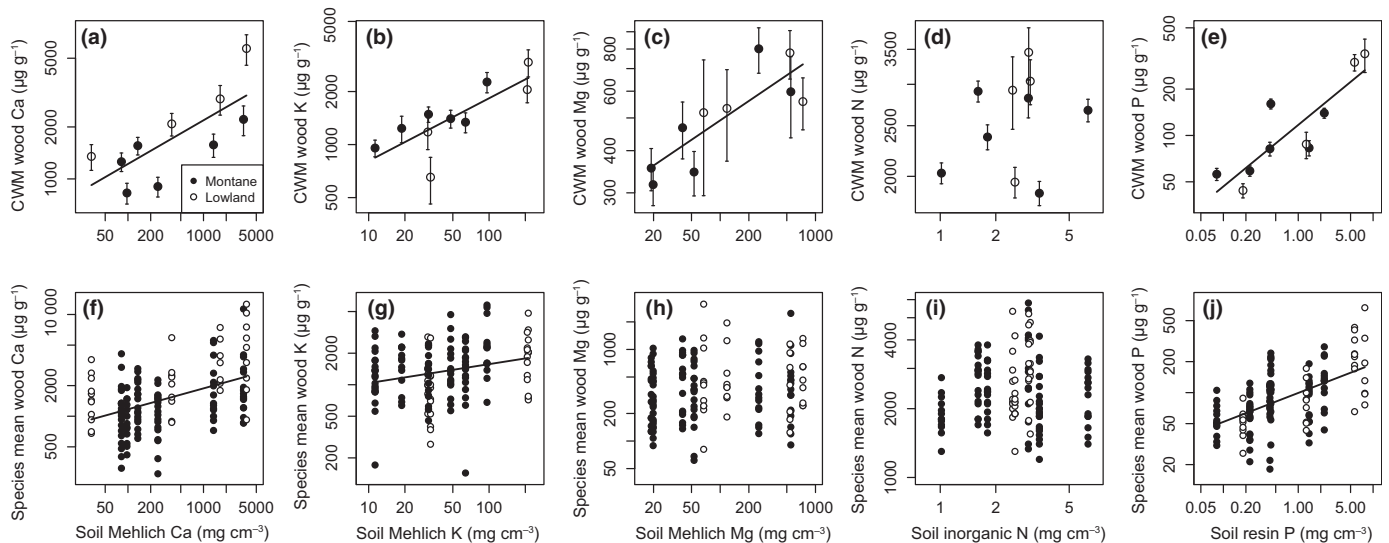| Nutrient | Community weighted means ($\mu g\ g^{-1}$) | | | Species means ($\mu g\ g^{-1}$) | | |
|---|---|---|---|---|---|---|
| | Mean | Min | Max | Mean | Min | Max |
| Calcium (Ca) | 2038 | 823 | 5692 | 2082 | 271 | 12 613 |
| Potassium (K) | 1547 | 653 | 2935 | 1622 | 157 | 5771 |
| Magnesium (Mg) | 526 | 320 | 807 | 492 | 61 | 3123 |
| Nitrogen (N) | 2603 | 1857 | 3454 | 2557 | 1300 | 5800 |
| Phosphorus (P) | 135 | 44 | 339 | 111 | 19 | 668 |
| N : P | 34 | 14 | 59 | 35 | 4 | 181 |
| Carbon (C) : N | 203 | 148 | 267 | 209 | 80 | 381 |
| C : P | 7276 | 2175 | 14881 | 7510 | 729 | 50 400 |



**Fig. 2** Wood nutrient concentrations (of the outer 5 cm of sapwood) vs soil nutrient availability in four lowland (open circles) and six montane (closed circles) forest plots in Panama. Soil nutrients were measured in the top 10 cm of soil and are expressed in volumetric units (mg cm$^{-3}$). Lines of log–log linear regression models are presented where the relationship between wood and soil nutrients is significant. (a–e) Community weighted mean (CWM) wood nutrient concentrations of all species sampled in each plot. Y bars, one basal area-weighted standard error. (f–j) Species mean wood nutrient concentrations plotted as a function of plot-level soil nutrient concentrations. Axes are plotted on log scales. See Methods section for soil nutrient extraction protocols.
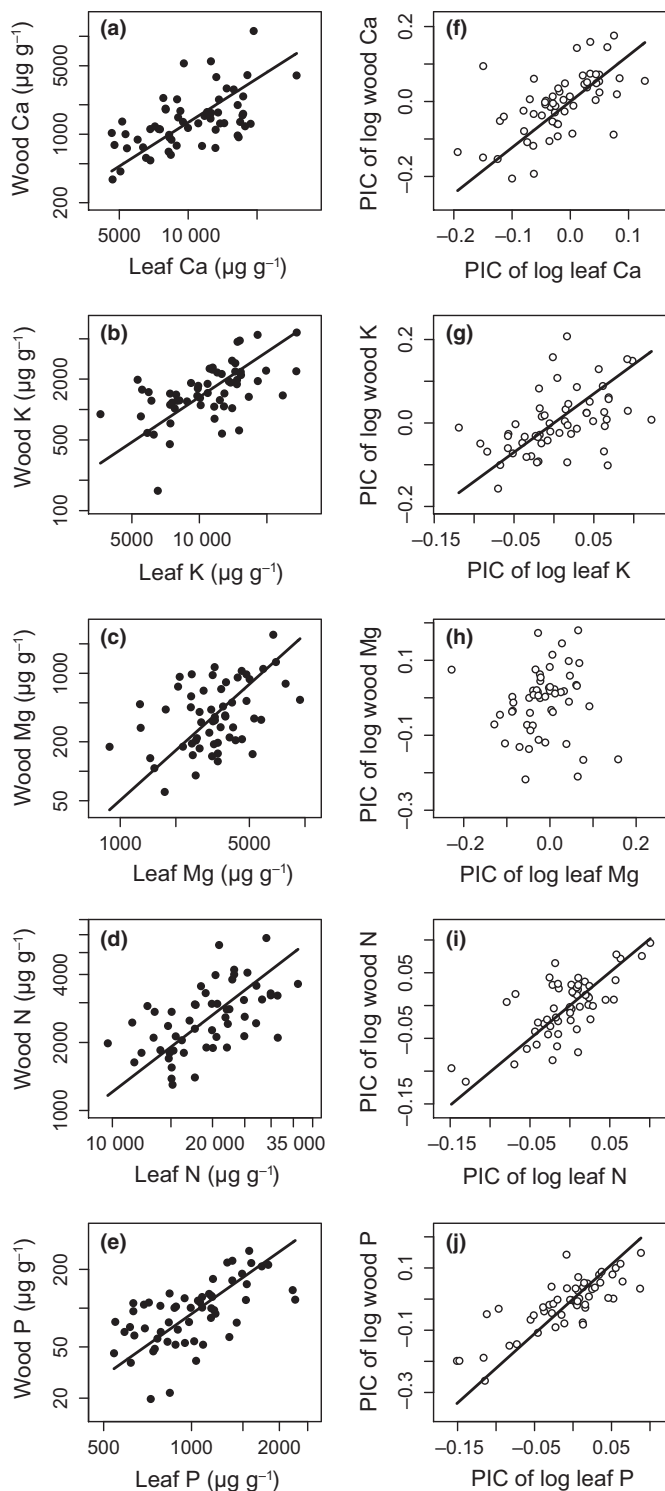
**Fig. 3** Scaling relationships of species mean leaf and wood nutrient concentrations for 58 tree species sampled in western Panama. Lines represent major axis regression model fits. Scaling relationships were fit for log-transformed observed species mean wood and leaf nutrient concentrations (a–e; closed circles) and for the phylogenetically independent contrasts (PIC) of logged species mean values (f–j; open circles). Wood nutrients were analyzed for the outermost 5 cm annulus of sapwood.

## Wood nutrient concentrations vs wood density

We did not find support for the hypothesis that wood nutrient concentrations increase with wood density. Species mean wood density significantly declined as species mean wood P increased and was not significantly associated with any other wood nutrient (Table 4). Wood Ca, K, Mg, N and P were all significantly positively correlated with one another at critical $\alpha = 0.05$ (Table 4). After correcting for multiple comparisons, Ca was significantly correlated with only N and P, and Mg was correlated with only P (Table 4).

Correlation of the PICs of species woody traits gave qualitatively similar results to analysis of observed values at $\alpha = 0.05$, except that PIC of wood Mg was negatively correlated with PIC of wood density (Table S3). After correcting for multiple comparisons, PIC of wood P remained significantly correlated with all wood traits; however, the relationships of wood Ca, Mg, and N with wood K were no longer significant, and wood Mg was no longer correlated with wood Ca or wood density (Table S3).

## Radial variation in wood nutrients

In the 110 tree cores examined, the concentration of macronutrients in the outermost 5 cm of wood was strongly positively correlated with nutrient concentrations in the adjacent 5–10 cm segment for all elements (Fig. 4; Table S4). Nutrient concentrations in the outer segment explained a greater proportion of the variance than the inner segment for Ca ($r^2 = 0.74$), Mg ($r^2 = 0.77$) and N ($r^2 = 0.75$) compared to K ($r^2 = 0.53$) and P ($r^2 = 0.61$). For K, N and P in MA regression models, intercept of the inner vs outer relationship was significantly $< 0$ and the slope was significantly $> 1$ (Table S4), indicating that inner segments have lower concentrations of K, N and P on average than the outer segments at low element concentrations. However, this discrepancy between segments declines or reverses with increasing element concentration (Fig. 4). For 88 of 110 individuals, the outer core segment had a higher wood P concentration than the inner core segment. The Ca and Mg inner vs outer regression parameters did not significantly differ from a 1 : 1 relationship (Table S4).

Species varied in the magnitude and the direction of radial differences in nutrient concentrations between outer and inner annuli. Of the elements examined, radial patterns in wood P were most qualitatively consistent across species, because 14 of 18 species had significantly higher P concentrations in the outer vs inner core. Wood P concentrations declined by 35% from the outer to inner segments across all species, although species mean radial P discrepancies ranged widely from 2% to 88% (Fig. 5). By contrast, Ca and Mg concentrations were significantly lower in the outer compared to the inner core for the majority of species (Fig. 5), and the magnitude of this difference exceeded 50% for four of 18 species. However, qualitatively distinct radial cation differences were present in other species (Fig. 5). For wood N and K, there were similar numbers of species with radial differences $< 0$, $= 0$, or $> 0$.

## Discussion

### Variation in wood nutrients among species and sites

Wood nutrient concentrations varied substantially among 106 tree species sampled along a regional soil fertility gradient in Panama. For some nutrients, observed values encompassed the entire range of wood nutrient concentrations reported in tropical tree species to date. Wood N concentrations (Table 2) fell within the range of values reported previously for tropical forest species (400–6900 $\mu g\,g^{-1}$; Becker *et al.*, 2012; Mascaro *et al.*, 2012; Martin *et al.*, 2014). The same was true for the observed range of species mean wood Ca concentrations in this study, which fell within the range of the values reported for sapwood in the Meerts (2002) meta-analysis of 93 temperate and tropical angiosperm species (60–15 000 $\mu g\,g^{-1}$). By contrast, the range in wood P concentrations observed (19–668 $\mu g\,g^{-1}$) here exceeded the range of previously reported for sapwood P concentrations in wild angiosperms (20–615 $\mu g\,g^{-1}$; Meerts, 2002; Mascaro *et al.*, 2012). The range in species wood K and Mg observed here exceeded the maximum previously reported values for sapwood K (160–4500 $\mu g\,g^{-1}$) and Mg (80–1290 $\mu g\,g^{-1}$) reported in Meerts (2002). Furthermore, the average of species mean wood Ca, K and P concentrations in this study all exceeded the 'typical range' of wood nutrient concentrations reported in Chave *et al.* (2009), which is a frequently cited reference for wood traits, indicating that calculations of forest wood nutrient stocks based on this review may be underestimated.

Community weighted mean (CWM) wood nutrient concentrations also differed widely among plots, and paralleled soil nutrient availability for all elements except N. Because the concentrations of macronutrients strongly covaried in both woody

**Table 3** Major axis regression model fits of the scaling relationship between observed species mean wood and leaf nutrient concentrations (log(leaf) ~ log (a) + log(wood) × b) and the phylogenetically independent contrasts (PICs) of species mean wood and leaf concentrations (PIC of log leaf ~ PIC of log wood × b) for 58 tree species sampled at Fortuna Forest Reserve

| Nutrient | Model | n | Intercept: log (a) | | | Slope: b | | | $r^2$ | P |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | Mean | 2.5 | 97.5 | Mean | 2.5 | 97.5 | | |
| Calcium (Ca) | Observed | 58 | −10.61 | −5.35 | 1.36 | 1.93 | 1.36 | 3.00 | 0.33 | <0.001 |
| | PIC | 56 | | | | 1.40 | 0.99 | 2.10 | 0.36 | <0.001 |
| Potassium (K) | Observed | 58 | −11.03 | −22.30 | −5.33 | 1.97 | 1.36 | 3.19 | 0.30 | <0.001 |
| | PIC | 56 | | | | 1.92 | 1.24 | 3.50 | 0.24 | <0.001 |
| Magnesium (Mg) | Observed | 58 | −17.72 | −45.64 | −8.76 | 2.93 | 1.82 | 6.39 | 0.18 | <0.001 |
| | PIC | 56 | | | | 5.61 | 1.95 | −8.14 | 0.03 | 0.223 |
| Nitrogen (N) | Observed | 58 | −4.47 | −11.45 | −0.35 | 1.25 | 0.83 | 1.95 | 0.31 | <0.001 |
| | PIC | 56 | | | | 1.01 | 0.84 | 1.23 | 0.49 | <0.001 |
| Phosphorus (P) | Observed | 58 | −10.03 | −17.42 | −5.99 | 2.10 | 1.52 | 3.17 | 0.36 | <0.001 |
| | PIC | 56 | | | | 2.22 | 1.85 | 2.67 | 0.54 | <0.001 |

**Table 4** Major axis regression model fits of pairwise combinations of log-transformed species mean wood nutrient (calcium (Ca), potassium (K), magnesium (Mg), nitrogen (N) and phosphorus (P); $\mu g\,g^{-1}$) and wood density (WD; $g\,cm^{-3}$) measured in 76 tree species from six forest sites at Fortuna (df = 74)

| x variable | y variable | Intercept | | | Slope | | | $r^2$ | $P^1$ |
|---|---|---|---|---|---|---|---|---|---|
| | | Mean | 2.5 | 97.5 | Mean | 2.5 | 97.5 | | |
| WD | Ca | −11.2 | 32.9 | 0.4 | 31.8 | 11.7 | −44.5 | 0.02 | 0.249 |
| | K | 21.2 | 12.9 | −22.5 | −24.1 | 51.5 | −9.7 | 0.02 | 0.179 |
| | Mg | 18.7 | 11.8 | −96.1 | −22.2 | 176.2 | −10.4 | 0.04 | 0.081 |
| | N | 16.8 | 10.8 | −2.1 | −15.7 | 17.1 | −5.3 | 0.01 | 0.302 |
| | P | 10.9 | 8.2 | 25.4 | −11.2 | −36.2 | −6.6 | 0.10 | 0.005* |
| Ca | K | 2.21 | −2.75 | 5.22 | 0.70 | 0.29 | 1.39 | 0.10 | 0.006* |
| | Mg | −2.73 | −21.42 | 2.53 | 1.18 | 0.46 | 3.78 | 0.07 | 0.024* |
| | N | 5.90 | 4.85 | 6.88 | 0.26 | 0.12 | 0.41 | 0.16 | <0.001** |
| | P | −0.03 | −3.60 | 2.44 | 0.62 | 0.28 | 1.12 | 0.12 | 0.002** |
| K | Mg | −5.86 | −23.11 | −0.34 | 1.60 | 0.84 | 3.97 | 0.11 | 0.005* |
| | N | 5.42 | 4.15 | 6.58 | 0.32 | 0.16 | 0.50 | 0.18 | <0.001** |
| | P | −2.10 | −4.93 | −0.06 | 0.90 | 0.62 | 1.29 | 0.30 | <0.001** |
| Mg | N | 6.65 | 5.82 | 7.45 | 0.19 | 0.06 | 0.34 | 0.10 | 0.007* |
| | P | 0.61 | −1.14 | 1.99 | 0.66 | 0.42 | 0.96 | 0.26 | <0.001** |
| N | P | −11.72 | −17.61 | −8.02 | 2.08 | 1.60 | 2.84 | 0.41 | <0.001** |

[1]P values: *, significant at P < 0.05; **, significant correcting for multiple comparisons (P < 0.0033).
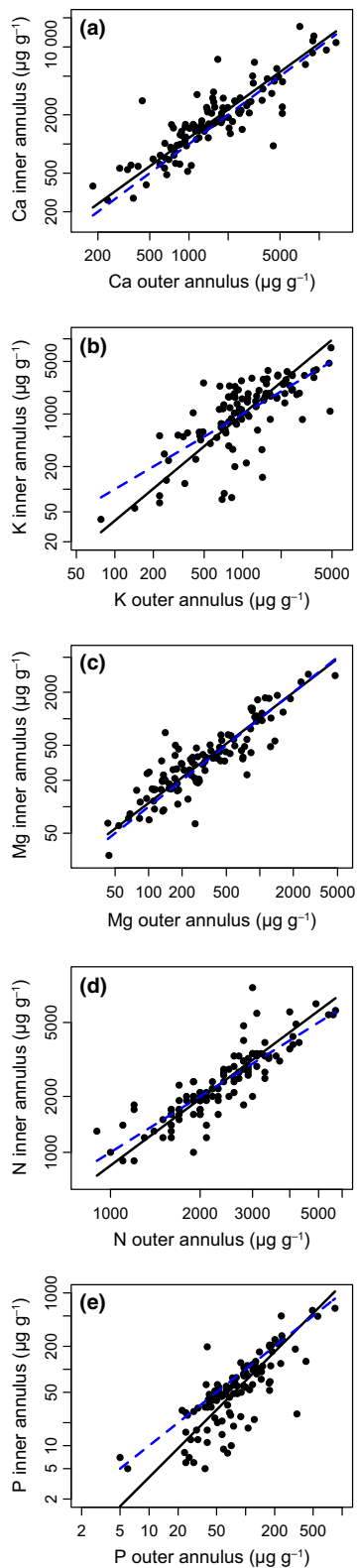
**Fig. 4** Scaling relationship of nutrient concentrations in 'outer' 5 cm of annulus of wood and adjacent 'inner' 5–10 cm annulus for 110 trees cored in Panama. Black lines represent major axis (MA) regression model fits of the scaling relationship between nutrient concentrations in inner and outer (log(inner) ~ log($a$) + log(outer) × $b$). Blue dashed lines represent a 1 : 1 relationship.

biomass and the soil available pools, it is difficult to determine if the ecosystem sequestration of nutrients in woody biomass is proportional to the soil availability of each nutrient independently, or if the increases in the availability of one limiting element increases the uptake of nonlimiting elements to maintain stoichiometric balance (Marschner, 1995). For example, CWM wood N might correlate significantly with soil P, but not soil N, because N investment in wood is constrained by P limitation. By contrast, the Stability of Limiting Nutrients Hypothesis (Han *et al.*, 2011) would posit that the low variability in wood N among species and along environmental gradients is evidence that N is more limiting than other elements, because increased availability of limiting elements should result in increased growth, not increased tissue nutrient concentrations. Given that a long-term factorial nutrient addition experiment in the Panama canal watershed has found that N, P and K all limit aspects of plant growth (Kaspari *et al.*, 2008; Wright *et al.*, 2011), and that responses to N addition in western Panama vary among species (Adamek *et al.*, 2009), it seems likely that numerous interacting forces influence the uptake and subsequent sequestration of individual nutrients in wood. Nonetheless, the result that rock-derived macronutrients in wood generally track the availability of these nutrients in the soil has implications for ecosystem and community processes.

Although soil nutrient concentrations were strong predictors of community mean wood nutrients at the plot level, wide variation in species mean nutrient concentrations in a given habitat suggest that species were unlikely to be excluded completely from a habitat based on nutrient allocation patterns, either physiologically or competitively. However, comparison of the slopes of wood vs soil regression models indicates that basal area CWM wood nutrient values are more sensitive to soil nutrient variation than the unweighted average across species, providing evidence that tradeoffs related to nutrient allocation underlie shifts in species abundance across soil gradients. Alternatively, this pattern could occur if canopy trees differ systematically in wood nutrient allocation from smaller stature trees. In a Jamaican montane forest, Tanner (1985) attributed the significantly lower nutrient concentrations of taller trees relative to short trees as a potential reason that tall trees were able to attain high biomass on nutrient impoverished soils. For 42 tree species in Bolivia, maximum tree height has been linked to wood anatomical traits including wood density, vessel diameter, and hydraulic conductance (Poorter *et al.*, 2010), which could have indirect effects on wood nutrient uptake and storage. Given that dominant canopy species disproportionately influence estimates of forest aboveground biomass (Slik *et al.*, 2013; Bastin *et al.*, 2015), efforts to quantify forest nutrient stocks in living biomass should prioritize the sampling of species with high basal area in a given community.

The strength of the relationship between species mean wood nutrient concentrations and soil nutrients were strongest for Ca and P, which were also the soil nutrients most closely associated with tree species distributions in lowland Panama (Condit *et al.*, 2013). This pattern provides evidence that differences among species in the acquisition and use of Ca and P is partially
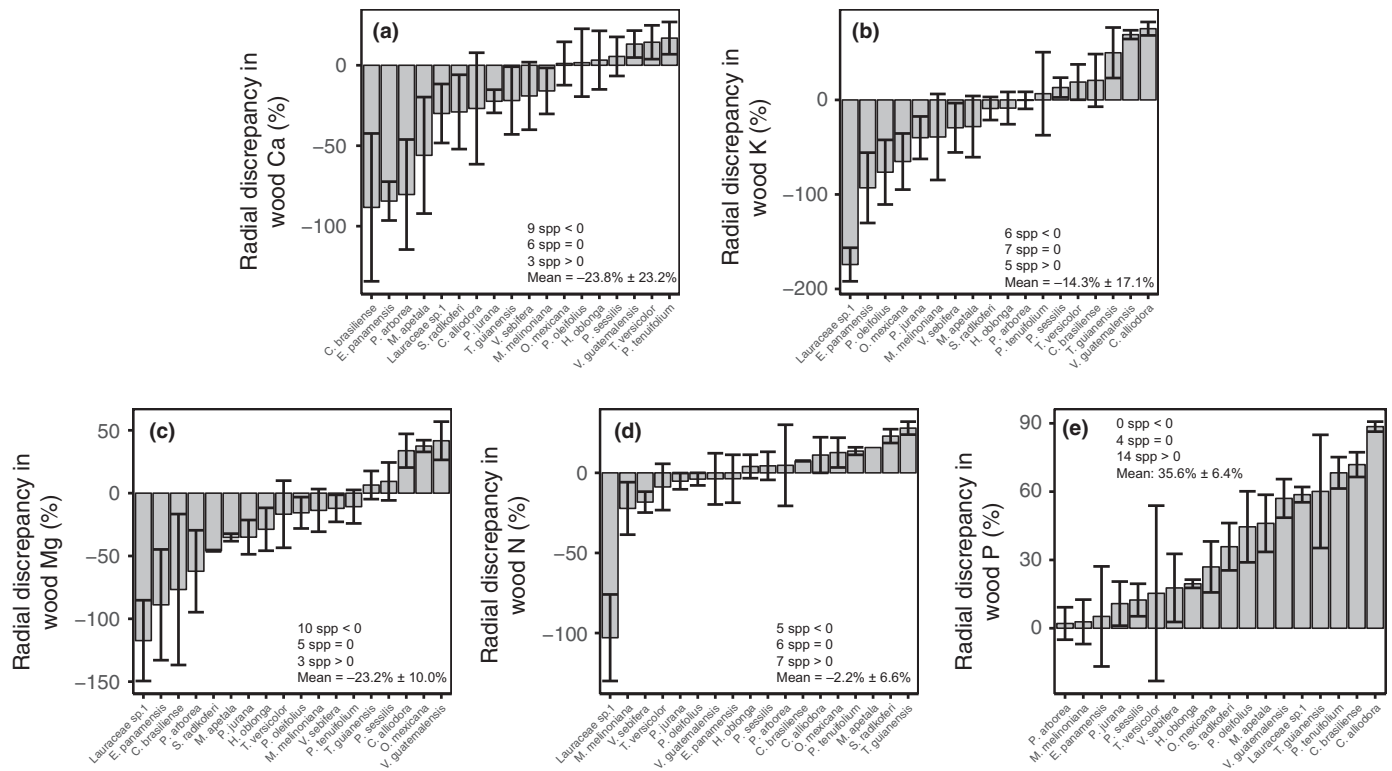
Fig. 5 Species mean radial discrepancy in calcium (Ca), potassium (K), magnesium (Mg), phosphorus (P) and nitrogen (N) concentrations (a–e) between the outermost annulus of the stem (0–5 cm in depth) and the adjacent inner annulus (5–10 cm in depth) for 18 tree species in Panama. Radial discrepancy was calculated as (outer − inner)/outer × 100. Species mean values ± SE are reported in each panel.

responsible for their distribution across edaphically heterogeneous landscapes. Small within-species sample size and high species turnover among sites prevented us from assessing how much of this response was explained by taxonomic or environmental controls. In Amazonian tree species, foliar P and Ca concentrations are more sensitive to environmental variation in soil availability than N and Mg concentrations (Fyllas *et al.*, 2009), and experimental nutrient addition in tropical forests show that both foliar and wood P concentrations respond more strongly to nutrient addition than do N concentrations (Harrington *et al.*, 2001; Ostertag, 2010; Schreeg *et al.*, 2014; Mo *et al.*, 2015). Wood Ca and P may also be more sensitive than other elements to soil conditions due to respective variation in the soil available nutrient pools, because the ranges of soil available Ca (115-fold) and P (90-fold) were vastly greater than the variation in Mg (38-fold), K (20-fold) and inorganic N (sixfold) among the 10 plots sampled (Table 1). However, the heterogeneity in Ca and P in this region may provide a basis for the evolution of tradeoffs in Ca and P allocation strategies to optimize fitness in high vs low resource environments. Similarly, foliar P is the primary leaf trait differentiating tree species adapted to habitats differing widely in soil nutrient availability in Borneo (Baltzer & Thomas, 2010). Therefore, P allocation may be a key component of edaphic specialization niches in tropical regions worldwide. In regions with less spatial variation in soil nutrient availability than Borneo or Panama, weaker selection for tradeoffs in nutrient allocation might results in less variation among species and sites in wood nutrient concentrations.

## Wood–leaf nutrient scaling

The scaling relationship between species mean wood and leaf tissues was significant for all nutrients for species examined along the Fortuna nutrient gradient, supporting findings of previous meta analyses which have shown that N and P allocation is constrained across plant organs (Kerkhoff *et al.*, 2006; Ågren, 2008). However, our results differ from previous observations that wood and leaf nutrients concentrations are not closely correlated within angiosperm taxa (Pietsch *et al.*, 2014; Zanne *et al.*, 2015). Significant scaling between the PICs wood and leaf Ca, K, N and P indicate that the apparent functional coordination of nutrient allocation across organs is not simply a consequence of evolutionary history. Although wood and leaf nutrients are correlated for all elements, the shape of scaling relationships differed among nutrients. Nonlinear scaling of wood and leaf nutrients for all elements except N indicated that leaf nutrients are more constrained than wood nutrients at high concentrations, perhaps because allocation of nutrients to woody repositories increases when nutrients are no longer limiting to photosynthesis. The dynamics of N storage may differ from other elements because plants generally store N as organic amino acids or proteins (Chapin *et al.*, 1990) and the storage of organic N may incur a substantial carbon cost relative storage of inorganic molecules (Millard, 1988). By contrast, for P, which can be stored as inorganic phosphate in vacuoles (Sinclair & Vadez, 2002), the wood-leaf scaling exponent was *c.* 2, meaning that, for example, a 10% increase in foliar P corresponds to a 20% increase in wood P. The apparent

accumulation of P in wood at high foliar P concentrations may reflect the evolutionary importance of P storage reserves. Compared to other macronutrients, P is particularly immobile in soil solution and is spatially and temporally variable in its availability to plants (Lambers *et al.*, 2008). This indicates that trees may be under selection to allocate excess P to storage to mitigate P limitation when the P demands of plant growth exceed P supply from soil.

## Correlation of wood nutrients with life history parameters

We did not find support for the hypothesis from the wood economics spectrum (WES) that wood nutrient storage increases with wood density (Chave *et al.*, 2009). These results are in contrast to the findings of Martin *et al.* (2014) in which wood N was positively correlated with wood density along this axis in tree species in the Panama Canal watershed, but corroborate the findings of Becker *et al.* (2012), who found no relationship between wood N and wood density among tree species in Uganda. Given that wood and leaf nutrients were positively correlated, wood nutrients likely reflect whole plant allocation strategies or access to soil resources rather than active allocation of nutrients to wood storage reserves at the expense of other organs. In fact, wood P declined with increasing wood density in our montane forest, suggesting that low biomass P concentrations and dense wood are traits related to the survival of tropical tree species on low fertility habitats. Although previous studies have reported that tree communities on low fertility soils have higher wood density (Muller-Landau, 2004; Chave *et al.*, 2006) and lower wood P concentrations (Tanner, 1985) than communities on more fertile soils, this study is the first to our knowledge to test a functional relationship between these traits in tropical tree species. The significant relationship between the PICs of wood density and wood P indicate that this pattern is not solely a consequence of evolutionary history and might represent coordinated evolution of traits that facilitate survival on low resource habitats.

## Radial variation in wood nutrient concentrations

Wood nutrient concentrations of the outermost 5 cm of the trunk strongly predicted nutrient concentrations of the adjacent inner segment for all nutrients, suggesting that radial variation in wood nutrients does not qualitatively influence patterns of interspecific or intersite variation in wood nutrients. Retranslocation of P from sapwood as it transitions to heartwood appears to be widespread among Panamanian trees, because wood P was lower in the inner annulus than the outer annulus for 76% of individuals cored. Although this study did not evaluate differences between heartwood and sapwood explicitly, our results are consistent with Meerts (2002), who found that heartwood concentrations were significantly lower than sapwood concentrations for 59 of 64 tree species. Radial variation in wood Ca, K, Mg and N concentrations were more idiosyncratic across species. Although Meerts (2002), a dataset of predominately temperate species, found that wood N and K concentrations were higher in sapwood than heartwood for the majority of species, there was no consistent pattern across species or individuals for these elements in our study. Given that the increased remobilization efficiency of P compared to N from senesced leaves is used as a primary indicator that tropical forests are more P-limited than temperate forests (Vitousek, 1984), the increased retranslocation efficiency of P from sapwood relative to other elements may be evidence that the trees in our study were primarily P-limited. Because trees retain metabolically inactive wood in their stems, retranslocation of nutrients may be easier to quantify at the tree and species level in wood cores than in leaf litter, and should perhaps be utilized more often in studies of plant nutrient dynamics. Furthermore, if radial P translocation is greater in tropical forests than other ecosystems, it may exacerbate the allometric decline in whole-plant N : P and C : P ratios (Elser *et al.*, 2010), which are used to calculate ecosystem nutrient stocks. As this study provides only a cursory evaluation of radial variation in wood nutrients, studies explicitly examining both the effect of continuous radial variation and heartwood/sapwood status on wood nutrients across species and sites are needed to improve our understanding of the function of wood nutrients.

## Ecosystem implications of variation in wood nutrients

The marked variation in wood nutrient concentrations both among and within soil habitats observed here reinforces the idea that a trait-based approach using species-specific nutrient data could improve estimates of ecosystem processes in diverse tropical forests (Cornwell *et al.*, 2008). The scaling relationships of wood and leaf nutrients suggest that leaf nutrient values in global plant trait databases have the potential to be used to assign wood nutrient content used in models predicting carbon turnover from woody biomass (Cornwell *et al.*, 2009). Given that tissue nutrient concentrations may be more important than wood anatomy and exogenous environmental factors in determining wood decomposition rates (Zanne *et al.*, 2015), the eightfold range in community mean wood P concentrations observed here could translate to substantial differences in carbon residence time along fertility gradients. Not only are wood nutrient concentrations important for predicting the dynamics of coarse woody debris, but also nonlinear scaling of species wood and leaf P concentrations suggest that trees store excess P in wood, which has implications for how tropical trees will respond to future global change scenarios. Understanding the extent to which P can be remobilized from woody tissues could improve predictions of how the growth of tropical trees will respond to the alleviation of other limiting factors via $CO_2$ fertilization and N deposition.

## Conclusions

Wood stores more biomass than any other plant organ, and the fate of carbon and nutrients in the wood of tropical trees has particularly important implications of global biogeochemical cycles. Our study is among the first to demonstrate the enormous variability in wood nutrient concentrations among tropical tree species, and the strong relationship between community mean

wood nutrients and soil resource availability. These results suggest that allocation of limiting nutrients to woody biomass is an important functional characteristic influencing species distributions and biogeochemistry along edaphic gradients in tropical forests.

## Author contributions

K.D.H. and J.W.D. designed research and sampling protocol. K.D.H. carried out field data collection. K.D.H. and B.L.T. participated in chemical analyses of plant tissues. B.L.T. contributed soil data for this study. K.D.H. wrote the manuscript with input from J.W.D. and B.L.T.

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## Supporting Information

Additional supporting information may be found in the online version of this article.

**Table S1** Species mean wood Ca, K, Mg, N and P concentrations for 106 trees species sampled in this study.

**Table S2** Summary of log–log linear regression models testing the relationship between community weighted mean (CWM) wood nutrient concentrations and soil nutrient availability and species mean wood nutrient concentrations and soil nutrient availability.

**Table S3** Major axis regression model fits of pairwise combinations of the phylogenetically independent contrasts (PIC) of species mean wood nutrient (Ca, K, Mg, N and P) and wood density (WD) measured in 76 tree species from six forest sites at Fortuna.

**Table S4** Major axis regression model fits of the scaling relationship between nutrient concentrations in the outermost 5 cm annulus of wood vs the adjacent 5–10 cm annulus of wood cores $(\log(\text{inner}) \sim \log(a) + \log(\text{outer}) \times b)$ for 110 trees in Panama.

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