

Wood nitrogen concentrations in tropical trees: phylogenetic patterns and ecological correlates

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Summary

- In tropical and temperate trees, wood chemical traits are hypothesized to covary with species' life-history strategy along a 'wood economics spectrum' (WES), but evidence supporting these expected patterns remains scarce. Due to its role in nutrient storage, we hypothesize that wood nitrogen (N) concentration will covary along the WES, being higher in slow-growing species with high wood density (WD), and lower in fast-growing species with low WD.
- In order to test this hypothesis we quantified wood N concentrations in 59 Panamanian hardwood species, and used this dataset to examine ecological correlates and phylogenetic patterns of wood N.
- Wood N varied > 14-fold among species between 0.04 and 0.59%; closely related species were more similar in wood N than expected by chance. Wood N was positively correlated with WD, and negatively correlated with log-transformed relative growth rates, although these relationships were relatively weak. We found evidence for co-evolution between wood N and both WD and log-transformed mortality rates.
- Our study provides evidence that wood N covaries with tree life-history parameters, and that these patterns consistently co-evolve in tropical hardwoods. These results provide some support for the hypothesized WES, and suggest that wood is an increasingly important N pool through tropical forest succession.

Introduction

A central goal in forest ecology is to understand the mechanisms driving life-history variation among co-occurring tree species. The links between morphological, physiological and chemical traits on the one hand, and life history parameters on the other, are critical for better understanding the mechanistic basis of many important ecological processes including: successional dynamics following natural or anthropogenic disturbances (Bazzaz, 1979; Bazzaz & Pickett, 1980), tree species coexistence (reviewed by Wright, 2002), and biogeographic patterns of tree species distributions and community assembly (McGill *et al.*, 2006; Westoby & Wright, 2006). Life-history variation in trees is described most definitively in terms of realized plant fitness – growth, mortality and reproduction rates – across environmental gradients (Ackerly *et al.*, 2000; Westoby & Wright, 2006). In seeking to understand the selective pressures driving life-history variation among species, ecologists have spent considerable effort in identifying key functional traits that act as mechanistic determinants of plant fitness.

Several dimensions of functional trait variation have emerged as important covariates of tree life-history parameters, including: leaf-level photosynthetic rates and related physiological and morphological traits (i.e. the 'leaf economics spectrum'; Wright

et al., 2004); reproductive traits such as seed size and seed output (Moles *et al.*, 2004); and tree size metrics (King, 1990; Thomas, 1996). More recently, it has been hypothesized that a 'wood economics spectrum' (WES; Chave *et al.*, 2009) describes patterns of covariation in wood anatomical and chemical traits that are likewise important determinants of tree functional biology. Interest in the WES has been promoted by studies finding significant correlations between wood density (WD), and species-level growth and mortality rates, with higher WD associated with long-lived, slow-growing shade tolerant species (Muller-Landau, 2004; Poorter *et al.*, 2008; Kraft *et al.*, 2010; Wright *et al.*, 2010). Similarly, WD has been shown to be a correlate of particular leaf traits (Wright *et al.*, 2007), and maximum tree size (Thomas, 1996). Together, such studies have suggested that WES traits (namely WD) could represent easily measurable surrogates for tree life-history strategy, a particularly appealing prospect for tropical forest ecologists because the presence of many co-occurring species makes it difficult to obtain estimates of species-level growth, mortality and reproduction rates (Wright *et al.*, 2003). However, recent studies have also found a lack of support for a generalized WES. For example, one comparative study found that xylem vessel size and density are essentially unrelated to WD (Zanne *et al.*, 2010), while another found that wood hydraulic properties were unrelated to WD (Poorter *et al.*, 2010); wood traits have also

been shown to vary orthogonally with respect to leaf economics traits (Baraloto *et al.*, 2010; Zanne *et al.*, 2010).

Relatively little attention has been given to understanding interspecific variation in wood chemical traits, despite these traits being hypothesized to covary along the WES (Chave *et al.*, 2009). Evidence that chemical traits do covary along the WES has been mixed. In previous studies of Panamanian hardwood species, we found that wood carbon (C), lignin and holocellulose concentrations were unrelated to either species' growth and mortality rates, or supposedly key functional traits including WD and maximum tree size (Martin & Thomas, 2011; Martin *et al.*, 2013). Although a few studies have reported positive relationships between wood C concentrations and WD, these relationships hold only when subsets of data are included in the analyses (Elias & Potvin, 2003; Becker *et al.*, 2012). Arguably the only wood chemical trait receiving consistent support as a correlate of life-history strategy, at least in saplings, is the concentration of nonstructural carbohydrates (NSC; Myers & Kitajima, 2007; Poorter & Kitajima, 2007), although this trait was not originally hypothesized to be a contributor to the WES (Chave *et al.*, 2009).

A wood chemical trait hypothesized to contribute to the WES but receiving little attention in published studies is wood nitrogen (N) concentration. Although present at relatively low concentrations (*c.* 0.1–0.6%) wood N exhibits high interspecific variation among co-occurring trees (Becker *et al.*, 2012; Mascaro *et al.*, 2012), is a significant predictor of wood decomposition rates (Weedon *et al.*, 2009), and cumulatively represents an important N pool in tropical forest ecosystems (Kauffman *et al.*, 1995; Liu *et al.*, 2003; Mascaro *et al.*, 2012). Moreover, based on the small amount of research that does exist, there is reason to expect that wood N is a significant correlate of life-history strategy in trees.

Wood N and tree life-history strategy can be expected to covary when considering a 'storage vs growth' tradeoff as a selective pressure driving interspecific variation in wood chemistry. This tradeoff is commonly invoked to explain interspecific variation in NSC concentrations. Greater investment in NSC by late successional species represents a low-cost investment (in terms of growth opportunity cost) that allows for increased resilience to stochastic or chronic stresses, such as branchfalls or light limitation (Kobe, 1997; Poorter & Kitajima, 2007). Analogously, late-successional species may invest in larger stored N pools in woody tissues (at the expense of growth) as a means to facilitate redeployment of leaves after branch or foliar losses (Zimmerman *et al.*, 1994), sustain reproductive output over a longer portion of their life cycle (S. C. Thomas, unpublished) and/or synthesize defenses against herbivores (Coley & Barone, 1996), characteristics that are more pronounced in late successional species than in early successional.

Studies linking wood anatomy and chemistry provide more direct reason to expect wood N concentrations vary with life-history strategy in trees. Parenchyma cells – in particular axial parenchyma – are one of the most important storage sites in woody tissues, and can store N-based compounds either as mobile N reserves, or as proteins and other live cell constituents needed to

accumulate and mobilize starch (and other metabolites) for osmotic adjustment (Carlquist, 2007). Early research on temperate trees found that N concentrations were positively correlated with the volume of parenchyma cells in wood (Cowling & Merrill, 1966; Merrill & Cowling, 1966). Parenchyma cells also maintain higher WD than other cell types (Taylor, 1969). It therefore follows that wood N could be positively associated with WD and, in turn, negatively associated with species' growth and mortality rates (Muller-Landau, 2004; Poorter *et al.*, 2008; Chave *et al.*, 2009). Additionally, studies on seasonal crop trees reported wood N concentrations that were significantly reduced during times of leaf flushing (O'Kennedy *et al.*, 1975; Kato *et al.*, 1984). By analogy, because fast-growing, early-successional tree species have faster rates of leaf turnover (Wright *et al.*, 2004; Baltzer & Thomas, 2007), they might also have lower wood N concentrations. Taken together, the following hypothesis emerges: slower growing tree species with high WD and low mortality rates will have higher concentrations of wood N when compared to faster growing species with low WD and high mortality rates. To our knowledge this hypothesis has not been explicitly tested in any set of co-occurring tree species.

There remain large uncertainties in the evolutionary patterns of wood chemical traits. If wood chemical traits are indeed part of a coordinated axis of biological variation in trees (*i.e.* the WES), they should be (1) similar among closely related taxa and show significant phylogenetic signal (*sensu* Blomberg *et al.*, 2003), and (2) exhibit correlated evolution with other key WES or functional traits (Felsenstein, 1985; Harvey & Pagel, 1991). However, there have been very few tests of evolutionary patterns for any wood chemical traits. In two previous studies we did not detect a phylogenetic signal in wood C concentration, nor was wood C concentration correlated significantly with other functional traits (Martin & Thomas, 2011; Martin *et al.*, 2013). Similarly, two other studies did not detect significant relationships between wood C and N concentrations (Telmo *et al.*, 2010; Becker *et al.*, 2012).

In the present study, we use field data collected in concert with a survey of wood C concentration among co-occurring tropical tree species (Martin & Thomas, 2011), to address four main questions: to what extent does wood N concentration vary among co-occurring tropical hardwood species? Are wood N concentrations more similar among closely related taxa? And do wood N concentrations correlate to, and show evidence of coordinated evolution with, species-specific vital rates, wood density or other ecologically important functional traits? If so, then is high wood N concentration associated with slow tree growth and high wood density, as predicted under a wood N storage hypothesis?

Materials and Methods

Field and lab methods

In August 2008, wood samples were collected from 59 hardwood tree species at the Pipeline Road site in Soberania National Park (SNP), Panama. SNP is a seasonal, second-growth, semi-deciduous lowland moist forest site in central Panama (9°10'N,

75°45'W) with canopy heights reaching 20–40 m. The forest at SNP receives an average rainfall of 2100 mm yr⁻¹, with a 4-month dry season occurring from December to April, and mean monthly temperatures of *c.* 27°C (Croat, 1978). At SNP a total of 205 individual wood cores were taken from 59 hardwood tree species, representing 46 genera and 27 families (Table 1). We selected species that were known to attain mature sizes ≥ 10 cm in diameter at 1.3 m aboveground (diameter at breast height (dbh)) that spanned a range of life-history strategies, with species-specific WD, and growth and mortality rates used an *a priori* indicator of species life-history strategy (Wright *et al.*, 2003). We also chose species that were relatively common in these forests: during the 2000–2005 census interval, species chosen for this analysis accounted for 30.9% of forest basal area for trees ≥ 1 cm dbh in the nearby (< 15 km) 50-ha forest dynamics plot located on Barro Colorado Island (BCI; 9°15'N, 79°8'W).

For each species in our dataset we extracted wood cores from 3 to 5 individuals, all of which were ≥ 10 cm dbh. During tree selection all efforts were made to avoid biases due to the presence of compression or tension wood, and therefore only individual trees with straight growth forms were sampled and all trees with crooked stems, substantial heart-rot or other forms of stem damage were excluded; when necessary cores were taken in directions parallel to slopes to avoid compression- and/or tension-wood biases. All cores were taken at breast height (1.3 m aboveground) using a 5.15-mm diameter increment borer, and placed in a freezer within 4 h of extraction to minimize loss of volatiles.

Due to considerable logistical constraints in sampling woody tissues across the entirety of a given tree, we use sapwood samples for our analysis here. Although there are general hypotheses suggesting that wood chemistry varies significantly within trees (Lachenbruch *et al.*, 2011), available empirical data suggest that in angiosperms sapwood N values provide a surprisingly strong approximation of N in heartwood. To our knowledge the only available published meta-analysis comparing wood N in sapwood vs heartwood of angiosperms (*n* = 47) was by Meerts (2002) who found that within a given species, sapwood N concentrations are only 0.06% greater than heartwood N concentrations (0.174 ± 0.078% vs 0.117 ± 0.05%, respectively); in an expanded analysis that included an additional nine gymnosperms (*n* = 56 total) the slope of the relationship between sapwood N and heartwood N did not differ significantly from 1 (Meerts, 2002). Similarly our ongoing study on temperate trees has found sapwood N explains 90.2% of the variation in heartwood N, with the relationship between these variables not differing significantly from a linear model with a slope of 1 and intercept of 0 (A. R. Martin, unpublished). Less information is available for other tissues, but sapwood N has been reported to covary linearly with N concentrations in branches and roots, with sapwood N values explaining 60–70% of the variation in N concentrations in these tissues (Merrill & Cowling, 1966; Andre *et al.*, 2010; A. R. Martin, unpublished). Studies have found that bark exhibits notable variation in N concentrations compared to other woody tissues (Wetzel & Greenwood, 1991); however, our analysis was not designed to examine bark traits *per se* because bark is commonly considered separately in studies of tree functional traits (Rosell

et al., 2014). Considering these factors, we believe that N concentrations in sapwood provide reliable and representative species-specific information for our analyses here.

Following transport of frozen samples to the University of Toronto, we first removed the outer portion of each wood core using a utility knife, to ensure portions of the core that may have been contaminated by the surface of the core borer did not bias our results. Each core was then ground to a fine powder using a Wiley Mill (no. 40 mesh), and divided into two drying treatments: one half was oven-dried at 110°C for 2 d, while the other was freeze-dried under a vacuum for 7 d using a Labconco 8-l freeze drying system (Labconco Co., Kansas City, MO, USA). For 13 of the 205 cores there was insufficient material for paired drying treatments, so only freeze-drying was performed. All dried samples were then analyzed for N concentrations using an ECS 4010 CN analyzer (Costech Analytical Technologies Inc., Valencia, CA, USA), using an ethylene diamine tetraacetic acid standard. Preliminary analysis found that drying treatment did not have a significant effect on wood N concentration (paired *t*-test: *t*₁₉₁ = 0.719, *P* = 0.43). Therefore, wood N concentrations per tree were calculated as the mean value of two replicates per core.

Statistical analysis – interspecific variation and phylogenetic signal in wood N

All statistical analyses were performed using R v. 2.10.1 (R Foundation for Statistical Computing, Vienna, Austria). We first used an analysis of variance (ANOVA) to test if wood N concentrations varied significantly among species. We then tested for phylogenetic signal in species mean wood N by calculating Blomberg's *K* statistic (Blomberg *et al.*, 2003) in the 'picante' R package (Kembel *et al.*, 2010). Detailed interpretations of Blomberg's *K* statistic can be found in several published accounts (Blomberg *et al.*, 2003; Kraft & Ackerly, 2010); however, in short, *K* > 1 indicates that a trait has a stronger phylogenetic signal than expected under a Brownian model of trait evolution, whereas *K* < 1 indicates a greater similarity in trait values across distantly related species than would be expected under a Brownian model of trait evolution. The significance of observed *K* values was assessed using a randomization procedure (see Blomberg *et al.*, 2003). Note that because a Brownian model of trait evolution entails phylogenetic signal, the randomization tests compares significance of our observed *K* to a null *K* distribution with no phylogenetic signal, where *K*_{null} ≪ 1 (Kraft & Ackerly, 2010).

The phylogeny used for analyses was based on a maximum likelihood reconstruction (D. L. Erickson, unpublished) dated using three plastid loci following Kress *et al.* (2009). The phylogeny included 1347 species from 15 separate forest dynamics plots established by the Centre for Tropical Forest Science, including 337 species in the nearby (< 15 km) 50-ha forest dynamics plot on Barro Colorado Island (BCI), Panama (9°15'N, 79°85'W). The taxa for BCI were pruned from the larger phylogeny after dating with PATHd8 (Britton *et al.*, 2007), and employed in current phylogenetic analyses. Before running *K* tests, we first used the 'APE' package in R (Paradis *et al.*, 2004) to prune the phylogenetic tree to include only those species that had associated

Table 1 Names, species codes corresponding to Fig. 1, sample size (n , number of cores for wood nitrogen (N)), mean wood N concentration (% mass basis \pm SE), wood carbon (C) : N ratio for 59 Panamanian tree species

Species	Code	n	Wood N	Wood C : N
<i>Alseis blackiana</i> (Rubiaceae)	ALSEBL	4	0.33 \pm 0.03	150.6
<i>Anacardium excelsum</i> (Anacardiaceae)	ANACEX	5	0.2 \pm 0.03	232.9
<i>Annona purpurea</i> (Annonaceae)	ANNOPU	3	0.23 \pm 0.04	198.4
<i>Annona spraguei</i> (Annonaceae)	ANNOSP	4	0.3 \pm 0.03	148.8
<i>Apeiba membranacea</i> (Tiliaceae)	APEIME	3	0.19 \pm 0.01	258.4
<i>Astronium graveolens</i> (Anacardiaceae)	AST2GR	3	0.23 \pm 0.02	188.5
<i>Bursera simaruba</i> (Burseraceae)	BURSSI	3	0.31 \pm 0.09	160.6
<i>Calophyllum longifolium</i> (Clusiaceae)	CALOLO	3	0.08 \pm 0.004	589.1
<i>Castilla elastica</i> (Moraceae)	CASTEL	3	0.32 \pm 0.05	147.1
<i>Cecropia obtusifolia</i> (Urticaceae)	CECROB	3	0.16 \pm 0.02	304.8
<i>Cecropia peltata</i> (Urticaceae)	CECRPE	3	0.16 \pm 0.01	287.0
<i>Ceiba pentandra</i> (Bombacaceae)	CEIBPE	4	0.27 \pm 0.004	172.0
<i>Chrysophyllum cainito</i> (Sapotaceae)	CHR2CA	5	0.35 \pm 0.11	127.3
<i>Croton billbergianus</i> (Euphorbiaceae)	CROTBI	3	0.19 \pm 0.02	240.0
<i>Croton draco</i> (Euphorbiaceae)	CROTDR	3	0.19 \pm 0.01	230.3
<i>Cupania latifolia</i> (Sapindaceae)	CUPALA	3	0.06 \pm 0.01	823.1
<i>Cupania rufescens</i> (Sapindaceae)	CUPARU	3	0.06 \pm 0.01	869.0
<i>Dalbergia retusa</i> (Fabaceae)	DALBRE	6	0.36 \pm 0.07	121.8
<i>Dendropanax arboreus</i> (Araliaceae)	DENDAR	5	0.16 \pm 0.03	277.8
<i>Faramea occidentalis</i> (Rubiaceae)	FARAOC	3	0.27 \pm 0.05	173.2
<i>Ficus insipida</i> (Moraceae)	FICUIN	3	0.31 \pm 0.05	148.8
<i>Guarea grandifolia</i> (Meliaceae)	GUARGR	3	0.09 \pm 0.004	541.7
<i>Guarea guidonia</i> (Meliaceae)	GUARGU	3	0.13 \pm 0.02	373.1
<i>Guarea 'fuzzy'</i> (Meliaceae)	GUARSP	3	0.22 \pm 0.02	200.0
<i>Guazuma ulmifolia</i> (Sterculiaceae)	GUAZUL	3	0.12 \pm 0.002	346.5
<i>Guettarda foliacea</i> (Rubiaceae)	GUETFO	5	0.34 \pm 0.04	140.1
<i>Gustavia superba</i> (Lecythidaceae)	GUSTSU	5	0.5 \pm 0.03	92.2
<i>Hirtella americana</i> (Chrysobalanaceae)	HIRTAM	5	0.22 \pm 0.03	214.9
<i>Hieronyma alchorneoides</i> (Euphorbiaceae)	HYERAL	6	0.17 \pm 0.04	282.0
<i>Hymenaea courbaril</i> (Fabaceae)	HYMECO	3	0.34 \pm 0.02	147.0
<i>Inga laurina</i> (Fabaceae)	INGAFA	3	0.16 \pm 0.02	310.6
<i>Inga oerstediana</i> (Fabaceae)	INGAMI	3	0.24 \pm 0.01	178.2
<i>Inga pauciflora</i> (Fabaceae)	INGAPA	3	0.23 \pm 0.01	205.4
<i>Inga pezizifera</i> (Fabaceae)	INGAPE	3	0.28 \pm 0.01	169.6
<i>Luehea speciosa</i> (Tiliaceae)	LUEHSP	3	0.23 \pm 0.03	213.4
<i>Macrocneum roseum</i> (Rubiaceae)	MACRGL	4	0.3 \pm 0.01	169.9
<i>Miconia argentea</i> (Melastomataceae)	MICOAR	3	0.17 \pm 0.01	288.7
<i>Miconia hondurensis</i> (Melastomataceae)	MICOHO	3	0.19 \pm 0.01	221.1
<i>Ochroma pyramidale</i> (Bombacaceae)	OCHRPY	4	0.17 \pm 0.04	299.3
<i>Ocotea puberula</i> (Lauraceae)	OCOTPU	3	0.2 \pm 0.01	241.0
<i>Ormosia amazonica</i> (Fabaceae)	ORMOAM	5	0.34 \pm 0.01	134.6
<i>Cinnamomum triplinerve</i> (Lauraceae)	PHOECI	3	0.13 \pm 0.01	363.6
<i>Platypodium elegans</i> (Fabaceae)	PLA2EL	3	0.59 \pm 0.02	84.7
<i>Poulsenia armata</i> (Moraceae)	POULAR	3	0.2 \pm 0.01	236.7
<i>Protium costaricense</i> (Burseraceae)	PROTCO	3	0.04 \pm 0.01	1360.8
<i>Protium tenuifolium</i> (Burseraceae)	PROTTE	3	0.04 \pm 0.03	1227.9
<i>Pseudobombax septenatum</i> (Bombacaceae)	PSE1SE	3	0.21 \pm 0.03	214.8
<i>Sapium glandulosum</i> (Euphorbiaceae)	SAPIAU	3	0.22 \pm 0.02	214.3
<i>Schizolobium parahyba</i> (Fabaceae)	SCHIPA	4	0.33 \pm 0.02	152.4
<i>Simarouba amara</i> (Simaroubaceae)	SIMAAM	3	0.22 \pm 0.02	230.8
<i>Tabebuia guayacan</i> (Bignoniaceae)	TAB 1GU	5	0.38 \pm 0.04	124.4
<i>Terminalia oblonga</i> (Combretaceae)	TERMOB	3	0.38 \pm 0.01	135.1
<i>Tetrathylacium johansenii</i> (Flacourtiaceae)	TET4JO	3	0.3 \pm 0.01	164.1
<i>Trichilia pallida</i> (Meliaceae)	TRI2PA	3	0.41 \pm 0.03	122.6
<i>Virola sebifera</i> (Myristicaceae)	VIROSE	3	0.38 \pm 0.06	128.4
<i>Virola multiflora</i> (Myristicaceae)	VIROSP	3	0.18 \pm 0.03	277.5
<i>Vochysia ferruginea</i> (Vochysiaceae)	VOCHFE	3	0.19 \pm 0.04	247.2
<i>Zanthoxylum ekmanii</i> (Rutaceae)	ZANTBE	3	0.33 \pm 0.02	155.1
<i>Zanthoxylum panamense</i> (Rutaceae)	ZANTP1	3	0.31 \pm 0.03	149.8

Wood C : N ratios were based on mean wood N values and mean wood C values from Martin & Thomas (2011).

wood N data. For analysis of the phylogenetic signal, we excluded eight species not in the phylogeny. The same method was also used to analyze K for all other functional traits (see Table 2). Lastly, to ensure that results from K tests performed on wood N data were not driven solely by the Fabaceae family (notable N-fixers), these tests were also performed on subsets of the dataset where (1) all *Inga* species were removed, and (2) all Fabaceae species were removed.

Statistical analysis – ecological correlates of wood N concentration

We evaluated if species' wood N concentration was a predictor of four ecological correlates: relative growth rates (RGR, % for trees ≥ 10 cm dbh), mortality rates (M, % for trees ≥ 10 cm dbh), maximum tree height (H_{\max} , m) and wood density (WD, g cm^{-3}). Species-specific RGR and M data were taken from Condit *et al.* (2006) and are expressed as percentages for trees ≥ 10 cm dbh at the BCI forest dynamics plot, derived from a Bayesian hierarchical model. H_{\max} values were available for 32 species in our dataset, with 28 of these values coming from two published datasets (King *et al.*, 2006; Wright *et al.*, 2010) and four values coming from an unpublished dataset provided R. Condit. All H_{\max} values derived from unpublished data were calculated following Wright *et al.* (2010), as the mean height for the tree largest trees by dbh per species. Published WD figures were available for 25 study species (Wright *et al.*, 2010), with WD for the remaining 34 species coming from unpublished data provided by S.J. Wright; both published and unpublished WD values were calculated using identical methodologies, and in nearly all cases cores used to measure WD were derived from the same trees cored for wood N analysis in our study. We also examined the relationship between wood N, wood C and volatile C concentrations (% w/w), with all wood C and volatile C data taken from Martin & Thomas (2011); C-based trait values were derived from the exact same trees used in our analysis here. Species values for H_{\max} , WD, wood C and volatile C all met assumptions of normality and were not transformed before analysis (KS test: $P \geq 0.137$), while RGR and M values were log-transformed before analysis (KS test on log-transformed values: $P = 0.05$ and $P = 0.271$, respectively).

Relationships between wood N and other vital rates (*sensu* Wright *et al.*, 2003) and functional traits were evaluated in both species-level and phylogenetic frameworks. We first used simple linear regression on species' trait values, to test the relationship between wood N concentrations and the six ecological correlates; for all of these analyses, wood N was treated as the independent variable. We then used phylogenetically independent contrasts (PIC) to test for patterns of correlated evolution among wood N and the six traits (Felsenstein, 1985). The phylogeny used for this analysis was the same as that used for our tests of a phylogenetic signal (Kress *et al.*, 2009). For the regression analysis on PIC values, all explanatory models were forced through the origin, because the direction of contrasts is arbitrary (Garland *et al.*, 1992). For each wood N by trait correlation tested, the number of species included in species-level and PIC regression analyses were the same; however, due to the limited ecological trait data

that were available, the sample sizes across traits differed (Table 2). Wood C data from Martin & Thomas (2011) were also used to calculate C : N ratios for each species, which showed the same phylogenetic patterns as wood N (Supporting Information Fig. S1). Relationships between ecological correlates and C : N ratios were qualitatively similar to those with wood N, but generally weaker (Fig. S2; Table S1). The C : N ratio data are presented in Table 1 and as Figs S1 and S2 and Table S1, but otherwise they are not discussed here.

In some instances, correlations among traits or between traits and vital rates may be driven in large part by pioneer species (e.g. the WD-M relationship found by Poorter *et al.*, 2008; their Fig. 2). Therefore, we also conducted all bivariate trait correlation analyses on wood N (species-level and PIC) on a subset of the data that excluded pioneer species. For this analysis we removed from the dataset *Cecropia obtusifolia* and all species showing a higher RGR than *C. obtusifolia*, namely, *Croton billbergianus*, *Miconia argentea*, *Ochroma pyramidale*, *Simarouba amara* and *Zanthoxylum ekmanii*.

Lastly, we analyzed the relationship among wood N concentrations and ecological variables in a species-level framework using principal components analysis (PCA) in the 'vegan' R package (Oksanen *et al.*, 2013). Our PCA included only species for which all ecological trait data were available ($n = 32$), and also excluded volatile C concentrations as a correlate because volatile C is incorporated into total wood C concentration values (Martin & Thomas, 2011); similarly wood C : N ratios were not included in this analysis.

Results

Interspecific variation and phylogenetic signal in wood N

Across the 59 Panamanian tree species wood N concentration averaged $0.24 \pm 0.01\%$ (SE) and showed >14-fold variation among species ($F_{58,146} = 7.589$, $P < 0.0001$), ranging from $0.59 \pm 0.02\%$ in *Platyopodium elegans*, to a low of 0.04% in *Protium costaricense* and *P. tenuifolium* (Table 1; Fig. 1). Interspecific variation in wood N (coefficient of variation = 45.5%) was greater than within-species variation (median coefficient of

Table 2 Phylogenetic signal of six functional traits and two vital rates in Panamanian hardwood trees

Trait	n	K	P value
Wood nitrogen (N) concentration	59	0.128	0.006
Log-wood carbon (C) : N ratio	59	0.147	0.003
Wood C concentration	59	0.036	0.617
Volatile C concentration	59	0.048	0.363
Maximum tree height (H_{\max})	32	0.276	0.045
Wood density (WD)	59	0.096	0.024
Log-relative growth rate (RGR)	49	0.086	0.063
Log-mortality rate (M)	49	0.067	0.169

Traits showing significant phylogenetic signal (following Blomberg *et al.*, 2003) are highlighted in bold, and relative growth and mortality rates were log-transformed before analysis.

variation = 18.4%). Across the phylogeny, wood N concentration showed significantly greater phylogenetic signal than would be expected by chance alone ($K=0.128$, $P=0.006$, $n=51$), indicating that closely related taxa show similar wood N concentrations (Fig. 1). For instance, mean wood N concentration differed by $\leq 0.02\%$ among congeneric species of *Cecropia*, *Croton*, *Cupania*, *Miconia*, *Protium* and *Zanthoxylum* (Table 1; Fig. 1). Similarly, four species of *Inga*, the most speciose genus in our dataset, differed by a maximum of 0.12% wood N: three of the four species (*I. oerstediana*, *I. pauciflora*, *I. pezizifera*) differed by only 0.04% (Table 1; Fig. 1). Species in the genus *Virola* (*V. multiflora* and *V. sebifera*) showed the largest variation in wood N among all congeneric species at 0.2%, equivalent to a two-fold difference (Table 1; Fig. 2). Apart from wood N, only H_{\max} ($K=0.276$, $P=0.045$) and WD ($K=0.096$, $P=0.024$) showed a significant phylogenetic signal (Table 2).

The Fabaceae family did not solely drive interspecific patterns. With all observations in the Fabaceae family removed, wood N still showed significant variation among species ($F_{49,122}=7.211$, $P<0.0001$), and significant phylogenetic signal both with all

Inga species removed ($n=48$, $K=0.194$, $P=0.005$), and with all species in the Fabaceae family removed ($n=45$, $K=0.163$, $P=0.011$). Although removing Fabaceae from the dataset reduced maximum observed wood N from $0.59 \pm 0.02\%$ (*P. elegans*) to $0.49 \pm 0.03\%$ (in *Gustavia superba*), mean wood N changed by only 0.01% ($0.24 \pm 0.01\%$ inclusive of Fabaceae, $0.23 \pm 0.01\%$ exclusive of Fabaceae).

Ecological correlates of wood N concentration

Among traits examined, species' RGR was the strongest correlate of wood N concentrations, with species of greater wood N concentrations being significantly associated with a lower RGR (with RGR log-transformed before analysis: $P=0.013$, adj. $r^2=0.106$; Table 2; Fig. 2e). Mortality rates were also negatively related to wood N concentrations, although this relationship was weak and not statistically significant (mortality rate log-transformed before analysis: adj. $r^2<0$, $P=0.383$; Table 3). Of the other ecological traits tested, wood N was also significantly positively related to WD across species ($P=0.037$, adj. $r^2=0.058$; Table 3; Fig. 2d).

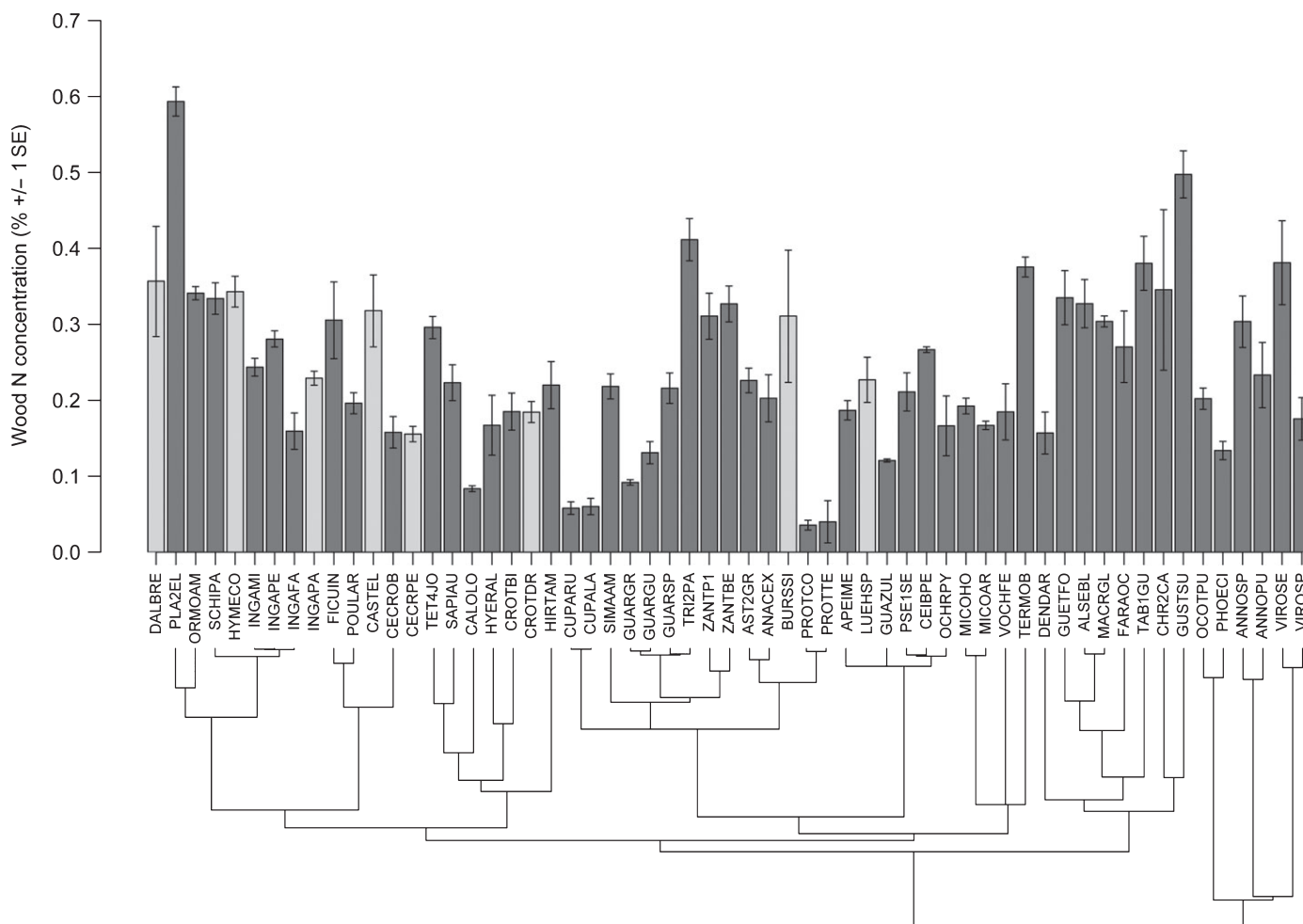


Fig. 1 Wood nitrogen (N) concentration in 59 Panamanian hardwood tree species. Species codes correspond to Table 1, and the phylogenetic tree represents the evolutionary relationships among species according to a maximum likelihood hypothesis reconstruction (D. L. Erickson, unpublished) dated using three plastid loci following Kress *et al.* (2009). Dark gray bars, species that were included in the phylogeny and thus used to test phylogenetic signal in wood N ($n=51$); light gray bars, species not included in the phylogeny and so were omitted from the test of phylogenetic signal ($n=8$).

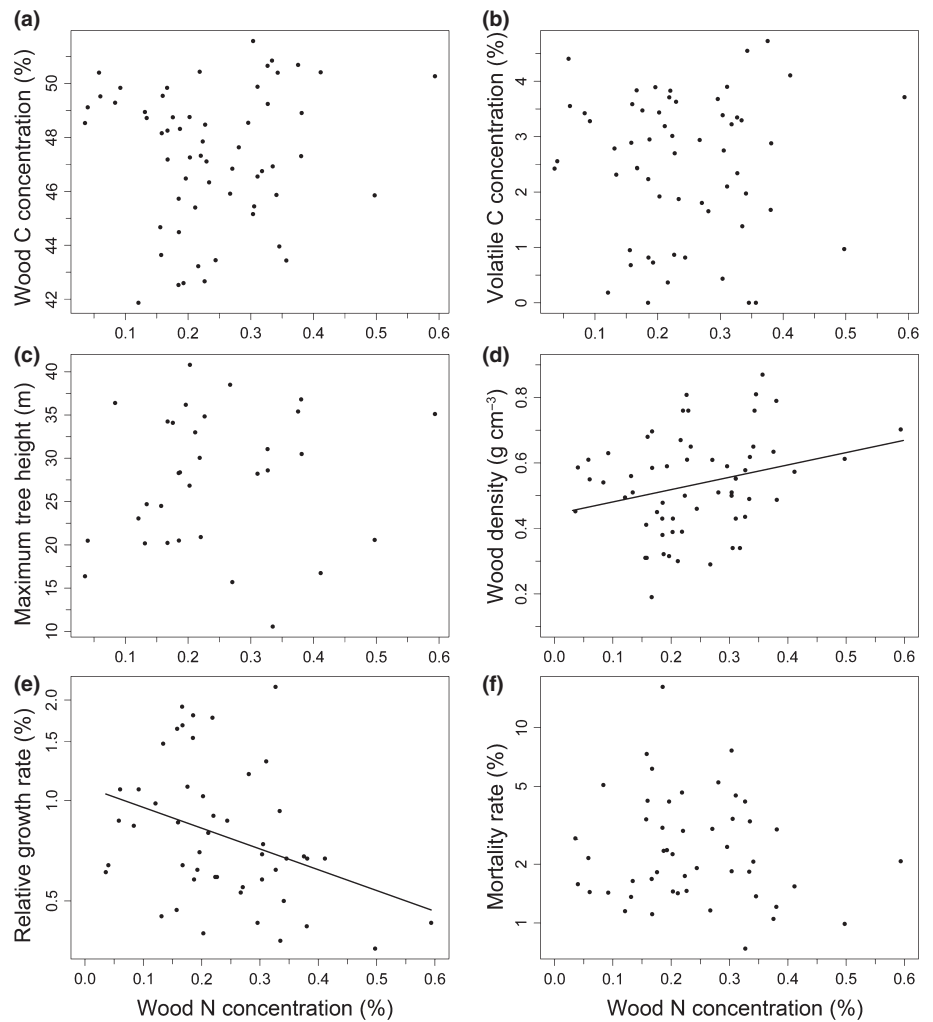


Fig. 2 Ecological correlates of wood nitrogen (N) concentration in Panamanian hardwood trees. Dark bold lines represent significant bivariate relationships ($P < 0.05$). Sample sizes, and model parameters and fits are presented in Table 2.

Table 3 Model parameters and coefficients of determination (r^2) and phylogenetically independent contrast (PIC) analyses of wood nitrogen (N) concentration as a predictor of four functional traits, as well as species' growth and mortality rates in Panamanian hardwood trees

Dependent variable	<i>n</i>	Correlation analysis			PIC analysis	
		Intercept (SE)	Slope (SE)	Adj. r^2 (model <i>P</i>)	Slope (SE)	Adj. r^2 (model <i>P</i>)
Wood C concentration (%)	59	47.0 (± 0.8)	1.3 (± 3.0)	< 0 (0.665)	3.9 (± 3.2)	0.009 (0.231)
Volatile C concentration (%)	59	2.5 (± 0.4)	-0.1 (± 1.6)	< 0 (0.971)	1.9 (± 1.5)	0.014 (0.196)
Maximum tree height (m)	32	25.7 (± 3.0)	7.5 (± 11.2)	< 0 (0.506)	1.2 (± 3.3)	0.029 (0.727)
Wood density (g cm ⁻³)	59	0.4 (± 0.1)	0.4 (± 0.2)	0.058 (0.037)	0.4 (± 0.1)	0.186 (0.001)
log-Relative growth rate (%)	49	0.1 (± 0.2)	-1.4 (± 0.6)	0.106 (0.013)	0.1 (± 0.1)	0.017 (0.185)
log-Mortality rate (%)	49	1.0 (± 0.2)	-0.7 (± 0.8)	< 0 (0.383)	1.6 (± 0.5)	0.157 (0.003)

Parameters are highlighted in bold for relationships that are statistically significant (where model *P* values ≥ 0.05).

Conversely, H_{max} , wood C and volatile C were unrelated to wood N concentrations (adj. $r^2 < 0$, $P \geq 0.506$; Table 3; Fig. 2a–c).

In addition to correlations between wood N and WD across species, there was also evidence of correlated evolution between these traits. Specifically, PIC values of wood N were significantly related to PIC values of WD ($P = 0.001$), explaining 18.6% of the variation (Table 3). A significant correlation between wood N and RGR was not detected when analyzed in a phylogenetic

framework (adj. $r^2 = 1.7$, $P = 0.185$; Table 3); however, there was a significant correlation between PICs of wood N and M (adj. $r^2 = 0.157$, $P = 0.003$; Table 3). As in analyses of species values, analysis of PIC values of wood C, volatile C and H_{max} did not show evidence of trait-correlated evolution (adj. $r^2 \leq 0.029$, $P \geq 0.196$; Table 3).

The two significant trait correlations found in the full dataset (Fig. 2; Table 3) were generally consistent when pioneer species

were removed. With pioneers removed, wood N was still significantly related to log-transformed RGR ($P=0.007$, $n=43$) and showed slightly higher explanatory power (adj. $r^2=0.15$ vs 0.106 with pioneers: Table 3). With pioneers removed, the correlation between wood N and WD became only marginally significant ($P=0.051$, $n=53$) but the explanatory power was nearly identical to the dataset inclusive of pioneers (adj. $r^2=0.054$ and 0.058, respectively). Significant relationships among PICs, however, were sensitive to the removal of pioneer species. With pioneers omitted from the dataset, PIC values of wood N were unrelated to PICs of WD (adj. $r^2 < 0$, $P=0.358$) and log-transformed mortality rates (adj. $r^2 < 0$, $P=0.794$).

Multivariate trait coordination

The first two principal components axes explained a total of 52.7% of the variation in six ecological traits (Fig. 3). The first principal components axis explained 32.1% of the total variation in traits, and was significantly positively associated with wood N concentrations (adj. $r^2=0.414$, $P<0.001$) and WD (adj. $r^2=0.253$, $P=0.002$), and significantly negatively associated with log-RGR (adj. $r^2=0.598$, $P<0.001$) and log-M (adj. $r^2=0.56$, $P<0.001$). The second principal axis explained an additional 20.6% of the variation and was significantly positively associated with H_{\max} (adj. $r^2=0.532$, $P<0.001$) and significantly negatively associated with both WD (adj. $r^2=0.383$, $P<0.001$) and log-M (adj. $r^2=0.119$, $P=0.03$).

Discussion

The wood economics spectrum (WES) was initially hypothesized to represent a critical axis of biological variation among trees

(Chave *et al.*, 2009), suggesting wood anatomical and chemical traits should covary with tree life-history strategy. Yet support for a generalized WES remains mixed, largely because of a near complete lack of information on the causes and consequences of variation in wood chemical traits among trees. We hypothesized that due to its potential role as a storage compound in wood, N concentrations should vary across species and track systematically with tree life-history strategies. We observed wood N concentrations to range widely across tropical tree species, varying 14-fold across the 59 Panamanian species tested here (Fig. 1; Table 1). Wood N concentrations were more similar among closely related taxa than expected by chance, a pattern that was not driven solely by notable N-fixing species in the Fabaceae family (Fig. 1; Table 1). To our knowledge our study is the first to show a significant phylogenetic signal in any wood chemical trait, for any set of tree species (Fig. 1; Table 2). Wood N was also correlated with life-history strategy in tropical trees, positively to species' WD and negatively to species' growth and mortality rates (Fig. 2); these patterns are generally consistent with the hypothesis that slow-growing, shade-tolerant species are selected for greater wood N due to the need for storage.

Wood N concentration as a correlate of life-history parameters in tropical trees

Although our analysis detected weak patterns between wood N concentrations and RGR, M and WD (Figs 2d–f, 3), existing research does suggest that these relationships may be attributable to the location where N-based compounds are stored in woody tissues. Data on this topic are limited, but studies suggest that a large proportion of N in wood is in the form of free amino acids, which are stored in ray and/or axial parenchyma cells (Cowling & Merrill, 1966; Merrill & Cowling, 1966; Kato *et al.*, 1984). In one analysis of 16 temperate and tropical hardwoods, total parenchyma volume explained 84% of the variation in wood N concentrations (Merrill & Cowling, 1966). It can thus be predicted that high-WD species (and hence slower growing species with low mortality rates; Kraft *et al.*, 2010) also contain more parenchyma cells per unit wood volume. Total parenchyma area and WD have been found to be positively, but not significantly, correlated in 42 Bolivian hardwood tree species (Poorter *et al.*, 2010). However, in 61 North and South American shrub species, axial parenchyma area was significantly positively associated with WD, while ray parenchyma area showed the opposite trend (Martinez-Cabrera *et al.*, 2009). By extension, the latter study suggests that axial parenchyma area may be the strongest predictor of wood N, and possibly the most important storage site of amino acids in wood. Further studies examining the relationship between both axial and ray parenchyma volume, wood N concentrations and chemical form of N in wood, could be important in understanding how chemical and anatomical traits are correlated along the WES.

Our results provide support for the role of wood N as a functional correlate of life-history strategy, but this is weak considering the strength of the correlations in our analysis (Fig. 2). The direction of the relationships between wood N and ecological

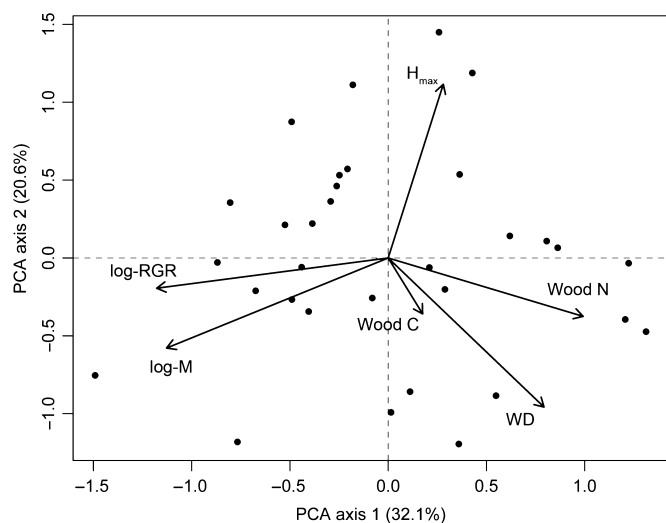


Fig. 3 Biplot illustrating multivariate relationships among wood nitrogen (N) concentrations and five life-history traits for 32 Panamanian tree species. Traits included in the principal components analysis (PCA) are wood density (WD), maximum tree height (H_{\max}), wood carbon (C) concentration, as well as two species-specific vital rates including log-transformed relative growth rate (log-RGR) and log-transformed mortality rates (log-M).

correlates (Fig. 2d–f) suggest that wood N contributes, at least partially, to a growth vs storage tradeoff among species. Taking these findings with existing studies, and considering our detection of significant evolutionary covariance between wood N and WD (Table 3), we suggest that traits related to nutrient storage in wood represent a coordinated dimension of the WES. Specifically, wood N (Figs 2, 3), wood NSC concentrations (Kobe, 1997; Poorter & Kitajima, 2007) and WD (Poorter *et al.*, 2008; Chave *et al.*, 2009), all receive support as correlates of life-history strategy in tropical and temperate trees. Explicitly examining correlations and coordinated evolution among wood N, NSC and WD would provide important insights into coordination of storage traits along the WES, but currently very little comparative research exists that addresses these patterns. In one Scandinavian conifer species (*Pinus sylvestris*), a small degree of seasonal covariation between wood N and wood NSC has been observed (Terziev *et al.*, 1997). Similarly, separate studies on two different temperate tree species found that both wood NSC and N concentrations changed significantly in response to stem damage (Kabeya & Sakai, 2005; Meyer *et al.*, 2008). These studies give some indication that these traits may show coordinated responses to selection pressures, but clearly further field research is needed to draw stronger conclusions.

Expanding our analysis to include other woody tissue types may also yield important insights into the functional significance of variation in wood N concentrations (cf. Baraloto *et al.*, 2010). Existing studies on how wood N concentrations vary across major woody tissue types including branches, roots, sapwood and heartwood are very limited, especially for tropical trees (Meerts, 2002). However, a number of studies from temperate trees have shown that bark plays a particularly important role in tree N dynamics, maintaining considerably greater N concentrations as compared to other woody tissues; a pattern ostensibly due to the role bark plays in protein storage (Wetzel & Greenwood, 1989). So while there is reason to expect that bark may play a role in driving life-history variation among species, to date bark chemistry *per se* has not been considered in comparative analyses of bark traits (Rosell *et al.*, 2014). Branch N concentrations have been shown to respond to reproductive output in masting trees (Sala *et al.*, 2012), although it is unclear if these patterns pertain to stem wood. Expanding analysis of wood N concentrations to include different woody tissue types could expand our understanding of wood chemical traits along the WES.

Our results also provide a compelling reason to examine wood chemical traits in relation to other suites of functional traits: namely, those traits associated with the leaf economics spectrum (LES; Wright *et al.*, 2004). Along the LES, tree species exhibiting high leaf N concentrations are commonly shade-intolerant species with high growth and mortality rates (Reich *et al.*, 1992; Wright *et al.*, 2004; Baltzer & Thomas, 2007), which is the opposite pattern to the one we observed here with wood N concentrations (Fig. 2e,f). So while leaf N concentrations are considered indicative of a species' resource capture strategy (Wright *et al.*, 2004), N concentrations in wood appear to be indicative of a species' position along a growth vs storage/defense strategy axis (Chave *et al.*, 2009).

Ecological implications of variation in wood N

The link between interspecific variation in leaf traits and patterns of N and P cycling has a history of conceptual and empirical support, both within and across forest types (Chapin, 1980; Reich *et al.*, 1992, 1997; Ordonez *et al.*, 2009). By comparison, the role of interspecific variation in wood chemistry for forest N stocks and fluxes has received very little attention (Vitousek & Sanford, 1986), likely because inputs of N from wood (1) are generally smaller in absolute terms compared to other sources of N (Hughes *et al.*, 1999), or (2) arrive as short-lived pulses from stochastic tree- or branch-fall events, rendering them difficult to quantify through time (Vitousek & Denslow, 1986; Liu *et al.*, 2003). A lack of data on species-specific wood N concentrations may also be limiting. Our results provide some evidence that in tropical forests, interspecific variation in wood N may explain some of the variation in observed changes in N availability through time. While our observed relationships were weak, our finding that wood N is generally greater in slow-growing, shade-tolerant species (Fig. 2d,e) suggests that variation in wood N across successional guilds may partially contribute to changes in N pools through time following canopy disturbance.

There is commonly a short-term transient release of N, followed by reduced availability, and then a gradual increase following localized disturbances such as treefalls (Vitousek & Denslow, 1986) and major disturbances such as fire or agricultural abandonment (Kauffman *et al.*, 1995; Hughes *et al.*, 1999). Leaf litter decomposition and its associated N mineralization is a major driver of these patterns (Denslow *et al.*, 1998; Hughes *et al.*, 1999); however, downed wood still can represent *c.* 4–20% of total aboveground N pools in primary and secondary tropical forests (Hughes *et al.*, 1999). Yet these figures may underestimate the relative contribution of wood N in old-growth forests. Following disturbance, recovery of leaf area index (LAI) occurs rapidly, often within 20 yr, ultimately saturating at values of 6–8 (Feldpausch *et al.*, 2005). Woody biomass accrual rates also decline with time since disturbance (Hughes *et al.*, 1999), but unlike LAI can continue to increase for many decades, even in ostensibly stable-state old-growth forests (Lewis *et al.*, 2009). Because woody biomass accruals through time will be largely from late-successional species with denser wood and higher N concentrations (Fig. 2d), woody tissues may continuously comprise a greater aboveground N pool through time.

Based on our data alone a general pattern of increasing wood N through succession remains speculative, particularly with respect to nutrient dynamics across highly diverse tropical forests; however, we would argue that this conjecture does frame an important rationale for expanding our analysis of wood N to a larger number of species. Specifically, incorporating species differences in wood N through time into simulation models could provide insights into the consequences of interspecific variation in wood N. For example, there is evidence that N-rich wood generally shows more rapid decomposition (Weedon *et al.*, 2009), likely because it provides a readily available source of nutrition for the development of mycelium, fruiting structures and spores in fungal decomposers (Cowling & Merrill, 1966). Following

disturbance, the presence of dead wood with high N concentrations (namely later-successional species; Fig. 2d–f) could contribute to higher post-disturbance soil N availability, because decomposing microbes will not be entirely reliant on plant-available forms of N from the soil for growth (Paul & Juma, 1981; Zimmerman *et al.*, 1995). The contribution of wood N to post-disturbance soil N dynamics could be a particularly important consideration in forests where disturbances are infrequent, occurring over relatively long return intervals. Our analysis provides some insights into these expected patterns (Figs 2, 3), but more data are clearly needed to evaluate the robustness of these predictions.

Conclusions

The WES (Chave *et al.*, 2009) provides a potential framework for conceptualizing the evolutionary processes responsible for interspecific variation in wood anatomical and chemical traits. To date research has not supported a generalized WES. However, based on our findings presented here and in related studies, we suggest that wood traits explicitly associated with nutrient storage – namely wood N, NSC concentrations and WD – form an important dimension of the WES. Research on correlations of storage-based traits, among one another and in relation to species growth and mortality rates, would be a critical step in evaluating evidence for a fully realized WES.

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Supporting Information

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

Fig. S1 Wood C : N ratios in 59 Panamanian hardwood tree species.

Fig. S2 Ecological correlates of wood C : N ratios in Panamanian hardwood trees.

Table S1 Relationships among wood C : N ratios and two functional traits and species' growth and mortality rates in Panamanian hardwood trees

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