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RESEARCH ARTICLE

Phylogenetic conservatism in the relationship between functional and demographic characteristics in Amazon tree taxa

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Abstract

1. Leaf and wood functional traits of trees are related to growth, reproduction, and survival, but the degree of phylogenetic conservatism in these relationships is largely unknown. In this study, we describe the variability of strategies involving leaf, wood and demographic characteristics for tree genera distributed across the Amazon Region, and quantify phylogenetic signal for the characteristics and their relationships.
2. Leaf and wood traits are aligned with demographic variables along two main axes of variation. The first axis represents the coordination of leaf traits describing resource uptake and use, wood density, seed mass, and survival. The second axis represents the coordination between size and growth. Both axes show strong phylogenetic signal, suggesting a constrained evolution influenced by ancestral values, yet the second axis also has an additional, substantial portion of its variation that is driven by functional correlations unrelated to phylogeny, suggesting simultaneously higher evolutionary lability and coordination.
3. *Synthesis*. Our results suggest that life history strategies of tropical trees are generally phylogenetically conserved, but that tree lineages may have some capability of responding to environmental changes by modulating their growth and size. Overall, we provide the largest-scale synopsis of functional characteristics of Amazonian trees, showing substantial nuance in the evolutionary patterns of individual characteristics and their relationships.

KEYWORDS
ecophysiology, functional traits, life history, macroecology, phylogenetic conservatism, tree physiology, tropical ecology

1 | INTRODUCTION

Life history theory predicts functional traits related to resource uptake, use and storage to be related to growth, survival and reproduction, following the live fast—live slow continuum (Díaz et al., 2016; Reich, 2014; Stearns, 1999). At one end of the spectrum, trees with larger (thinner) leaves and higher phosphorous and nitrogen content represent an acquisitive leaf function, prioritizing a rapid resource uptake (higher photosynthetic capability) and higher turnover (lower leaf lifespan) (Wright et al., 2004; but see Osnas et al., 2013). Such a trait combination will generally imply faster growth, leading to lighter wood with lower resistance to mechanical stress, which in turn may lead to higher mortality (Kraft et al., 2010). This strategy is often linked to rapid reproduction, where a higher number of smaller seeds are produced with a lower construction cost per seed unit (Adler et al., 2014; Poorter et al., 2008). In the tropics, taxa

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presenting these characteristics are typically identified as pioneers, with a higher capability to reach and rapidly colonize disturbed areas, as well as a lower tolerance to mechanical stress, herbivory and pathogens (Turner, 2001), and a prioritization of fecundity over longevity (Adler et al., 2014). At the other end of the spectrum trees have a conservative leaf function, with well-defended leaves with higher construction costs (longer leaf lifespan) but slower return on investment of nutrients (lower photosynthetic capacity) (Wright et al., 2004). This trait combination is most frequently associated with slower growth rates that result in denser and more resilient wood (Adler et al., 2014; Chave et al., 2009). Trees with this strategy often have higher investment per unit seed, which constrains the amount of seeds that a given individual can produce in a given year, but increases seed and seedling's probability to survive, including in shaded conditions (Moles & Westoby, 2006). This strategy may also be related with a longer lifespan, and then, lifetime seed production may be high even when presenting a low annual production (Moles, 2018). In the tropics, these genera are identified as stress-tolerant, prioritizing longevity over fecundity. Despite slower growth rates, they can reach bigger sizes through longer lifespans and greater resistance to disturbances (Turner, 2001).

The fast-slow continuum may not always hold however, particularly in the highly diverse tropics, where different combinations of functional traits may appear. This is the case of the coordination of leaf size and chemistry and the decoupling of wood and leaf traits (Baraloto et al., 2010; Fortunel et al., 2012). Trees with a slower return on investment of nutrients and dry mass in leaves can have a lighter wood while trees with a faster return on investment in leaves can present denser wood. It has also been shown that species with a fast strategy can also reach large sizes (long-lived pioneers) (Poorter et al., 2008; Rüger et al., 2018). Other studies have shown reproductive strategy to be independent of the fast-slow continuum and describe a growth-survival continuum (Salguero-Gómez et al., 2016) that is related to size and chance to become a reproductive individual, or adult (Rüger et al., 2018). Finally, some recent results show that the relationship between growth and mortality may not always be evident in the tropics (Russo et al., 2021) and that the fast-slow continuum does not capture the demographic strategy of long-lived pioneer species, especially important in the tropics (Rüger et al., 2020). Therefore, even if general patterns related to the fast-slow continuum seem to hold, some results suggest there may be a higher complexity in these hyper diverse ecosystems that may benefit from new analytical frameworks that move beyond an axis-decomposition perspective.

Accounting for evolutionary history, for example, with phylogenies, when analysing relationships between plant function and demography can also help clarify the meaning of these patterns, testing whether a given strategy appeared multiple times in recent evolutionary time (referred to as labile evolution) or whether it appeared in deeper evolutionary time and was subsequently maintained in descendants (referred to as conserved evolution). Individual traits related to leaf and wood function (Flores et al., 2014; Sanchez-Martinez et al., 2020) and to demography (Coelho de Souza et al., 2016) have been reported to show phylogenetic, or evolutionary, conservatism, as measured by phylogenetic signal (the degree of correlation between phylogenetic relatedness and trait value similarity). However, whether these patterns are independent for each trait or shared amongst traits cannot be elucidated from individual trait patterns, and individual trait patterns give little insight into process.

To address this issue, we quantify phylogenetic conservatism in trait correlations themselves, by quantifying the amount of correlation amongst traits that is related to phylogeny. When the correlation between a pair of traits is strongly related to phylogeny, this indicates that the correlation is present at both deep and shallow evolutionary timescales, that is, across ancestral lineages, genera and species, which we label as a pattern of phylogenetic conservatism and interpret as being due to constrained trait evolution. Alternatively, when trait correlations are independent of the phylogeny, processes leading to their covariation may be acting in more recent evolutionary timescales (e.g., across genera or species only) independently of their ancestry, pointing to a more labile, yet still coordinated evolution (Sanchez-Martinez et al., 2020). Thus, examining the phylogenetic structure of trait correlations can give greater insight into the evolutionary processes that have shaped trait variation amongst taxa than simply examining phylogenetic signal for individual traits one by one.

A quantification of phylogenetic conservatism in the correlations of functional traits and demographic characteristics in tropical tree taxa is still lacking, despite its heuristic value. Our study evaluates the evolutionary conservatism (or lack thereof) for Amazonian tree genera in the coordination of functional characteristics describing leaf function (resource uptake, use and storage) and wood function (resistance to stress, and size) with those describing demography (growth, reproduction and mortality). First, we describe the general trade-offs between functional and demographic characteristics in Amazonian tree taxa and quantify phylogenetic conservatism in the main axes of variation and their correlations. Then, we further explore the degree of phylogenetic conservatism in individual trait–trait correlations to extend the two-axis perspective.

2 | METHODS

2.1 | Data

We first assembled a list of all tree species present across the Amazon Basin Region within the ATDN network of 2186 plots, which span the major environmental gradients of the region (ter Steege et al., 2013, 2020) (see ter Steege et al., 2020 for a description of the dataset and its geographical extent). We compiled genus-level data on: (1) specific leaf area ($m^2 kg^{-1}$, specific leaf area)—related to photosynthesis and herbivore defence; (2) leaf nitrogen, phosphorous and carbon content ($g m^{-2}$, N, P, and C, respectively)—related to photosynthesis, nutrition and support function (Baraloto et al., 2010; Fortunel et al., 2012; Kattge et al., 2020; Kraft et al., 2008; Paine et al., 2012; Patiño et al., 2012); (3) wood density ($g cm^{-3}$)—related

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to mechanical support function; and (4) maximum diameter as a proxy of whole plant size (cm, $Diameter_{max}$)—related to structural support and access to light. We also compiled data on three functional characteristics related to demography: (1) maximum growth rate (cm $year^{-1}$, Growth $R._{max}$)—related to growth capability; (2) mortality rate (% of trees with diameter at breast height [DBH] >10 cm dying $year^{-1}$, Mortality *R.*)—related to lifespan (Coelho de Souza et al., 2016); and (3) seed mass (g)—related to reproductive potential (Foster & Janson, 1985; Hammond & Brown, 1995). As seed mass varies over several orders of magnitude, we used a logarithmic scale (Hammond & Brown, 1995; ter Steege & Hammond, 2001). We decided to use seed mass as a proxy of reproductive strategy based on its data availability and its widely reported positive relationship with seedling emergence and successful sapling recruitment (Henery & Westoby, 2001; Mazer, 1990; Moles & Westoby, 2006; Westoby et al., 1996). However, we acknowledge that seed mass may not fully represent the whole range of reproductive strategies. All variables were checked for normality, and mortality rate, maximum growth rate, and maximum diameter were subsequently log-transformed to improve normality.

We calculated genus-level mean trait values, and matched them with a previously published genus-level phylogeny (Neves et al., 2020) using the *ape* R package (Paradis & Schliep, 2019). Overall, we obtained trait values for 1036 genera which were represented in the phylogeny (Table S1 to see the number of genera with data for each trait). We focused our analyses at the genus level due to challenges with identification to the species-level in the tropics, particularly for trees where data are often collected from sterile individuals, that is, without flowers or fruits (Baker et al., 2017). Our analyses therefore focus on deep evolutionary patterns related to the diversification of genera in Amazon trees.

2.2 | Principal component analyses

We implemented principal component analyses (PCA) on leaf and wood functional traits (specific leaf area, leaf N, P, and C content, wood density and maximum diameter) and demographic characteristics (maximum growth rate, mortality rate and seed mass) separately and jointly (the latter referred to as the integrative PCA) using the *prcomp* function of the *stats* R package (R Core Team, 2020). In each case, plots showing the first principal components were generated using the *factoextra* R package (Kassambara & Mundt, 2020). Principal component analyses were conducted using those genera with complete observations for all the variables ($N = 197$). To ensure that the higher number of functional traits in relation to demographic characteristics did not affect the structure of the integrative PCA, we repeated the PCA using the same number of functional and demographic variables, keeping the functional traits with the lowest correlation values (specific leaf area, wood density and maximum diameter). Results did not differ (Figure S1). To test for the sensitivity of the integrative PCA to the taxa included, we performed a bootstrap procedure randomly sampling 95% of the data available and performed a PCA on that sample. This procedure was repeated 100 times. We show how the first principal components converge to similar values (Figure S2a–c) and that their difference with the PCA reported in the main text (i.e., using the whole dataset) is mainly distributed around zero (Figure S2d–f). Phylogenetic principal component analyses were also implemented by means of the *phytools* R package (Revell, 2009) to ensure that the structure of the PCA was similar with this approach (Figure S3). We acknowledge that using principal component analyses with a low number of variables may not be very useful in terms of dimensionality reduction. This could be the case particularly for principal components calculated for demographic characteristics (maximum growth rates, mortality rates, and seed mass). However, PCA was the best approach to extract orthogonal axis of variation related to function and demography, allowing us to focus on the correlation between these axes (i.e., correlation between main axes of variation related to different functional and demographic strategies). This allowed us to complement the trait-by-trait analyses with a more general evaluation of the coordination between functional and demographic axes.

2.3 | Phylogenetic Signal calculation

We estimated the level of phylogenetic conservatism for individual traits by calculating their phylogenetic variance, which is a measure of the amount of variance explained by the phylogenetic structure, ranging from 0 (no variance related to the phylogeny) to 1 (100% of the variance explained by the phylogeny). (Table S1). To do so, we used the *computeVarianceCovariancePartition* function of the package *TrEvol* (Sanchez-Martinez et al., 2024). That function uses Bayesian phylogenetic mixed models (BPMMs) from the *MCMCglmm* R package (Hadfield, 2010) to estimate phylogenetic variance (V_{phylo}, amount of variance in a given trait that is related to the phylogenetic structure) and residual variance (V_{res}, non-phylogenetically related variance). Phylogenetic signal is described as the amount of variance for a given trait that is related to the phylogeny, divided by the total trait variance (Pagel, 1999), and is calculated as it follows:

$$PS = \frac{V_{phylo}}{V_{phylo} + V_{res}}.$$

As the Bayesian framework operates with posterior distributions of estimates, we calculated phylogenetic signal for the posterior distributions of the variance portions, obtaining a distribution for each phylogenetic signal measure from which mean and credible intervals were calculated. *p*-Values related to the probability that the distribution contained zero were calculated in the TrEvol package, importing functions from the BayesR R package (Makowski et al., 2019).

2.4 | Correlation calculation

We calculated the total correlation between individual pairs of traits, which was then decomposed into a phylogenetically

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conserved portion and non-phylogenetically conserved portion by means of phylogenetic mixed models (Table S2). The two portions sum to the total correlation. The phylogenetically conserved correlation refers to the portion of the total correlation that is phylogenetically structured, while the non-phylogenetically conserved correlation is the portion of the total correlation that is independent of the phylogenetic structure. To calculate these coefficients we used the *computeVarianceCovariancePartition* function of the *TrEvol* package (Sanchez-Martinez et al., 2024), which uses BPMMs from the *MCMCglmm* R package (Hadfield, 2010) to partition the amount of variance–covariance on pairwise traits related to the genus-level phylogeny. Correlation coefficients are calculated as follows:

$$\text{Total correlation} = \frac{\text{COV}_{\text{phylo}}^{T1,T2} + \text{COV}_{\text{res}}^{T1,T2}}{\sqrt{\left(V_{\text{phylo}}^{T1} \times V_{\text{phylo}}^{T2}\right) + \left(V_{\text{res}}^{T1} \times V_{\text{res}}^{T2}\right)}},$$

$$\text{Phylogenetic correlation} = \frac{\text{COV}_{\text{phylo}}^{T1,T2}}{\sqrt{\left(V_{\text{phylo}}^{T1} \times V_{\text{phylo}}^{T2}\right) + \left(V_{\text{res}}^{T1} \times V_{\text{res}}^{T2}\right)}},$$

$$\text{Non} - \text{phylogenetic correlation} = \frac{\text{COV}_{\text{res}}^{T1,T2}}{\sqrt{\left(V_{\text{phylo}}^{T1} \times V_{\text{phylo}}^{T2}\right) + \left(V_{\text{res}}^{T1} \times V_{\text{res}}^{T2}\right)}},$$

where $\text{COV}_{\text{phylo}}^{T1,T2}$ and $\text{COV}_{\text{res}}^{T1,T2}$ are phylogenetic and non-phylogenetic (residual) covariances between two traits (T1 and T2), V_{phylo} and V_{res} are phylogenetic and non-phylogenetic (residual) variances for each trait. As with the analyses of phylogenetic signal, we obtained a distribution of correlation estimates in each case from which mean and credible intervals were calculated as well as a *p*-value related to the probability of the distribution containing zero. Correlation coefficients were calculated for each pair of traits as well as for each pair of principal components coming from distinct principal component analyses (i.e., using just leaf and wood functional traits vs. just demographic characteristics).

We acknowledge that some of the studied traits may present directional relationships (i.e., variability in one trait being the mechanism driving variability in others), which could be characterized, for instance, by means of phylogenetic comparative methods such as phylogenetic least squares (Symonds & Blomberg, 2014). We did not use this methodology because our main aim was to characterize phylogenetic conservatism in trait covariances, for which correlation frameworks are more suitable (Westoby et al., 2023). Future works elucidating the causal trait networks will help complement the correlation perspective, elucidating directional effects between functional and demographic traits.

We used the *plotVcv* and the *plotNetworks* functions of the *TrEvol* package (Sanchez-Martinez et al., 2024) to display phylogenetic signal and correlation results. In the latter case, the function calculates network metrics (He et al., 2020). These metrics are edge density (ED), describing the proportion of actual connections amongst nodes out of all possible connections, and the maximum and mean absolute correlation coefficient ($|r|_{\text{max}}$ and $|r|_{\text{mean}}$) as a measure of the strength of the correlation amongst traits. In this framework, high ED represents high coordination between all traits, and high $|r|_{\text{max}}$ and $|r|_{\text{mean}}$ represent networks with a higher dependence amongst related traits (He et al., 2020). We used the *plotData* function of the *TrEvol* R package to plot principal components on the phylogeny.

3 | RESULTS

3.1 | Functional traits and demography conform to two main axes of variation in Amazonian tree taxa

Wood and leaf functional traits (wood density, maximum diameter, specific leaf area, and leaf N, P, and C content) related to the whole plant economic spectrum (Reich, 2014) and demographic characteristics (maximum growth rate, mortality rate, and seed mass) conformed to two main integrative principal components, which summarized 51% of the total variance in demographic and functional characteristics. The first integrative principal component, explaining 31% of the variance, represented the trade-off between resource acquisitiveness versus longevity and investment per unit seed. High scores represented genera with higher wood density and lower specific leaf area, leaf N, and P content. These genera also tended to present higher seed mass and lower mortality rates. Low scores represented genera with lower wood density and higher specific leaf area, leaf N, and leaf P content. These genera also tended to present lower seed mass and higher mortality rates (Figure 1).

The second integrative principal component explained 20% of the functional variance and was mainly related to size (maximum diameter), leaf C content and maximum growth rates. High scores represented genera with larger sizes, higher leaf C content, and higher maximum growth rates. Low scores represented genera with smaller sizes, lower carbon content in leaves, and slower growth (Figure 1). The third integrative principal component explained 16.9% of the variance and showed a correlation between growth and mortality (Figure S4).

Principal component analyses based only on functional traits or only on demographic characteristics supported these general patterns. The first functional trait principal component, explaining 40% of the variance, represented the correlation between wood density and leaf economics (represented by specific leaf area, leaf N, and P content). The second functional principal component explained 20% of the functional trait variance and represented the correlation between maximum diameter and leaf C content (Figure S5a). The first demographic principal component, explaining 55% of demographic characteristics variance, described the negative correlation between seed mass and mortality rates. The second demographic principal component, explaining 27% of the variance was related to maximum growth rate (Figure S5b).

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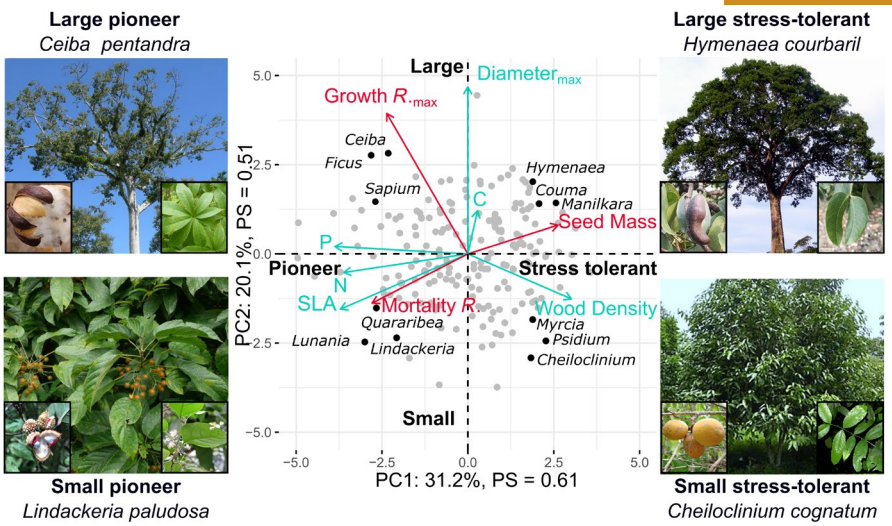

FIGURE 1 Functional, demographic, and integrative axis of variation. First principal components using leaf (specific leaf area; nitrogen, phosphorous, and carbon content, N, P, and C) wood (wood density, and maximum diameter, Diameter$_{max}$) and demographic characteristics (maximum growth rate, Growth $R._{max}$; mortality rate, Mortality *R.* and seed mass). Only genera with complete data for all variables are represented (197 genera). Variable contributions are shown as arrows, coloured in light blue (leaf and wood functional traits) and red (demographic characteristics). Principal-axis interpretation is shown in bold letters. Pictures of seeds (fruit when no seed images are available), leaves and whole trees for four species representing the four extreme strategies are shown. Phylogenetic signal and amount of variance explained by each axis in percentage are shown for each axis.

3.2 | Phylogenetic Signal in functional traits and demography

Individual functional traits had significantly non-zero phylogenetic variance (referred to as phylogenetic signal hereafter), ranging from 0.30 (mortality rates) to 0.79 (seed mass), and phylogenetic structure explained the majority of the trait variance (i.e., >50% or phylogenetic signal >0.5) for wood density, leaf N content, maximum diameter, and seed mass (4 of the 9 traits) (Figure 2b,c, pie charts, Table S1). The first two integrative principal components had Phylogenetic Signals of 0.61 and 0.51, respectively (61% and 51% of their variance was phylogenetically structured, respectively). The first and the second functional trait principal components, representing variability in leaf and wood functional traits, had Phylogenetic Signals of 0.45 and 0.51, respectively. The first and the second demographic principal components, representing variability in demographic characteristics, had Phylogenetic Signals of 0.42 and 0.51, respectively.

3.3 | Phylogenetic conservatism in the coordination of functional traits and demography

The phylogenetically conserved portion of trait-to-trait correlations was greater than the non-phylogenetic portion in 24 of the 27 significant correlations found (Figure S6; Table S2), consistent with the Phylogenetic Signal for integrative principal components summarizing overall functional trait and demographic variability.

Leaf functional traits (specific leaf area, leaf N, and leaf P) showed positive correlations with each other and were negatively correlated with wood density (Figure 2). These results describe how genera with larger and/or thinner leaves with greater N and P contents tend to have lower wood density while those with smaller leaves and/or thicker leaves with lower N and P contents tend to have a higher wood density. Maximum diameter was largely uncorrelated to leaf functional traits and wood density.

Positive correlations amongst specific leaf area, leaf N, and leaf P content showed both phylogenetically conserved and non-phylogenetically conserved portions. Meanwhile, leaf C content was correlated with leaf P and N content in a non-phylogenetically conserved manner. The coordination between leaf traits and wood density was attributed entirely to the phylogenetically conserved portion (Figure 2b,c), meaning that covariation between leaf and wood functional traits is phylogenetically structured.

Demographic characteristics also showed significant correlations, with some portions of those correlations showing phylogenetic structure. Mortality rate was positively correlated with maximum growth rate and negatively with seed mass. This result shows how genera with higher maximum growth rates and lower seed mass tend to have high mortality rates. The correlation between mortality rate and maximum growth rate showed no phylogenetic conservatism, while the correlation between mortality rate and seed mass showed a higher phylogenetic conservatism (Figure 2b,c).

Leaf and wood functional traits showed significant correlations with maximum growth rate, mortality rate, and seed mass, confirming results from the principal components analyses. Specific leaf area, leaf N, and leaf P content showed positive correlations with mortality rate and maximum growth rate and negative correlations with seed mass. Leaf C content showed only a low negative correlation with mortality rate and a low positive correlation with seed mass. Wood density was negatively correlated with mortality

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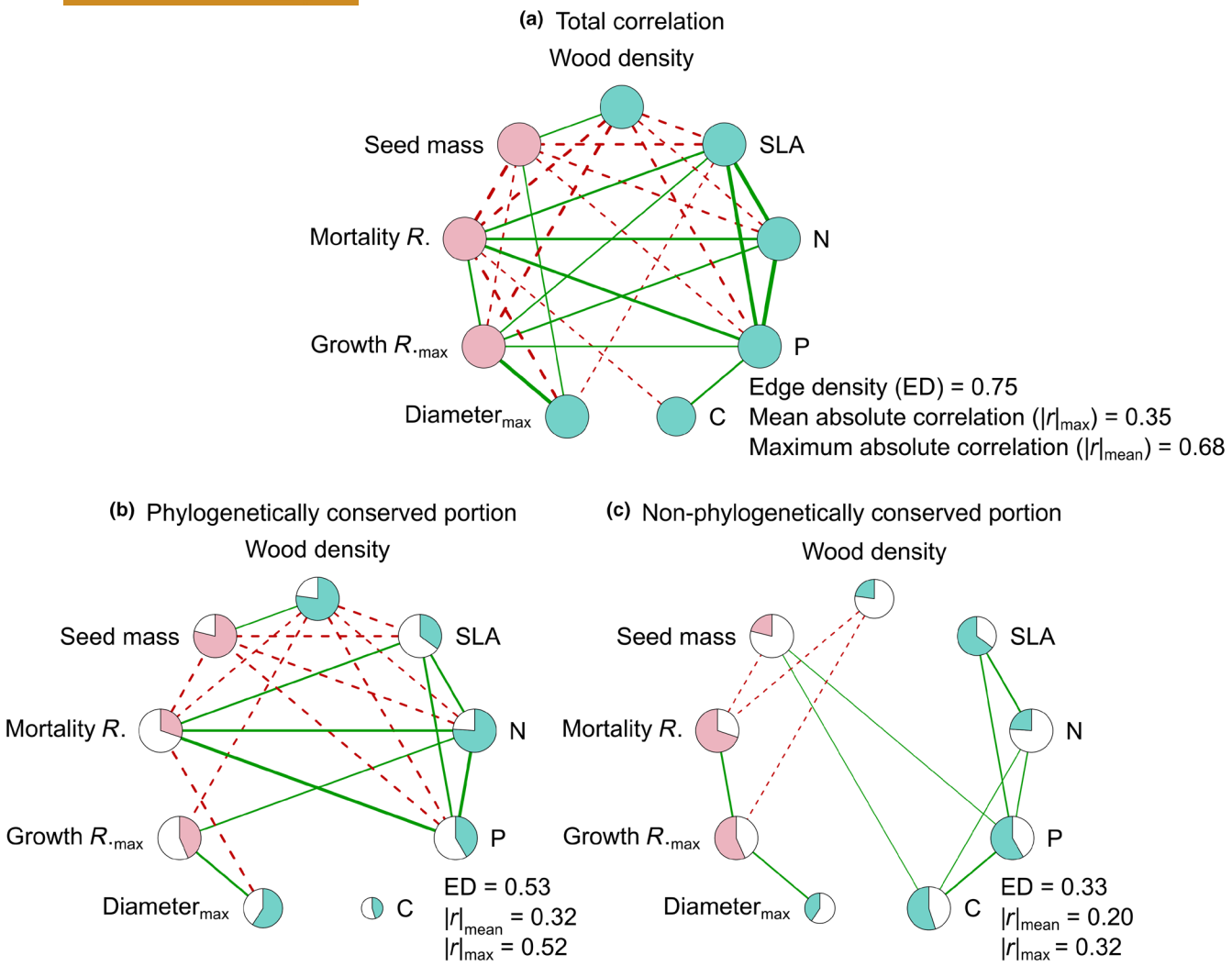

FIGURE 2 Variance–covariance networks. Trait correlation networks among leaf (specific leaf area; nitrogen, phosphorous and carbon content, N, P, and C), wood (wood density, and maximum diameter, Diameter_{max}) and demographic characteristics (maximum growth rate, Growth $R._{max}$; mortality rate, Mortality *R.* and seed mass). Leaf and wood functional traits are represented as nodes (circles) in light blue and demographic functional traits are shown in light red. Edges (lines connecting nodes) represent (a) total correlation, (b) phylogenetically conserved portion of the correlation and (c) non-phylogenetically conserved portion of the total correlation. Solid green lines represent statistically significant positive correlation coefficients and dashed red lines represent significant negative correlation coefficients. Line width is proportional to the absolute value of the correlation coefficient. Pie charts in b and c represent trait variance related to the phylogeny (i.e., phylogenetic signal) and trait variance not related to the phylogeny, respectively. Node size is proportional to the number of connections per node (i.e., degree). Three network metrics are shown in each case.

rate and maximum growth rate and positively correlated with seed mass. These results described how genera with larger and/or thinner leaves with greater N and P contents and low wood density tend to have higher maximum growth rate and mortality rate and lower seed mass. Genera with small and/or thicker leaves with lower N and P content and high wood density tend to have lower maximum growth rate and mortality rate and higher seed mass (Figure 2a). Maximum diameter was mainly positively correlated to maximum growth rate, but also showed a positive correlation with seed mass and negative correlation with mortality rate.

The correlations amongst leaf and wood functional traits and demographic characteristics showed a strong phylogenetic structure. However, there was some degree of independence from the genus-level phylogeny for some of these correlations. Correlations with significant non-phylogenetic portions were: the positive correlations of leaf C and P content with seed mass, the negative correlation of wood density with mortality rate and maximum growth rate, and the positive correlation of maximum diameter with maximum growth rate.

The trait-network approach allowed us to calculate network metrics describing the overall structure in the correlation matrix amongst functional and demographic characteristics. Network metrics clearly show that there is a higher structure in the phylogenetically conserved portion of the trait-to-trait correlation matrix. The trait network constructed using the phylogenetically conserved portion showed higher Edge Density (ED) and higher mean

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and maximum absolute correlation coefficients ($|r|_{mean}$ and $|r|_{max}$). A higher ED means there is a higher number of significant correlations amongst traits, that is, higher evolutionary integration.

To summarize the trait correlation network perspective, we also explored the correlation between the main axes of variation related to function and demography. To do so, we tested for phylogenetic conservatism in the correlation between the first two functional principal components obtained using leaf and wood functional traits and the first two demographic principal components obtained using demographic characteristics. The first functional component representing the negative correlation of specific leaf area, leaf P, and leaf N content with wood density (i.e., acquisitive to conservative resource-use strategies) was correlated to the first demographic component representing the negative correlation between mortality rate and seed mass (i.e., R to K reproduction and survival strategies). This correlation was explained entirely by the phylogenetically conserved portion of the correlation.

The second functional component representing the positive correlation between maximum diameter and leaf C content (i.e., small to large trees) was positively correlated to the second demographic component representing maximum growth rates. This correlation presented both phylogenetically conserved and non-phylogenetically, that is, evolutionarily labile, correlation portions (Figure 3). The first functional principal component was not correlated with the second demographic principal component, and the second functional principal component was not correlated with the first demographic principal component.

4 | DISCUSSION

4.1 | Leaf and wood function is coordinated with tree survival and reproduction, while stature is coordinated with growth in Amazonian tree taxa

Amazonian tree genera show a diverse range of relationships between functional traits and demographic characteristics, which can be aligned broadly along two axes of variation. The first axis describes the coordination between leaf and wood functional traits associated with carbon uptake and stress tolerance (Reich, 2014), highlighting

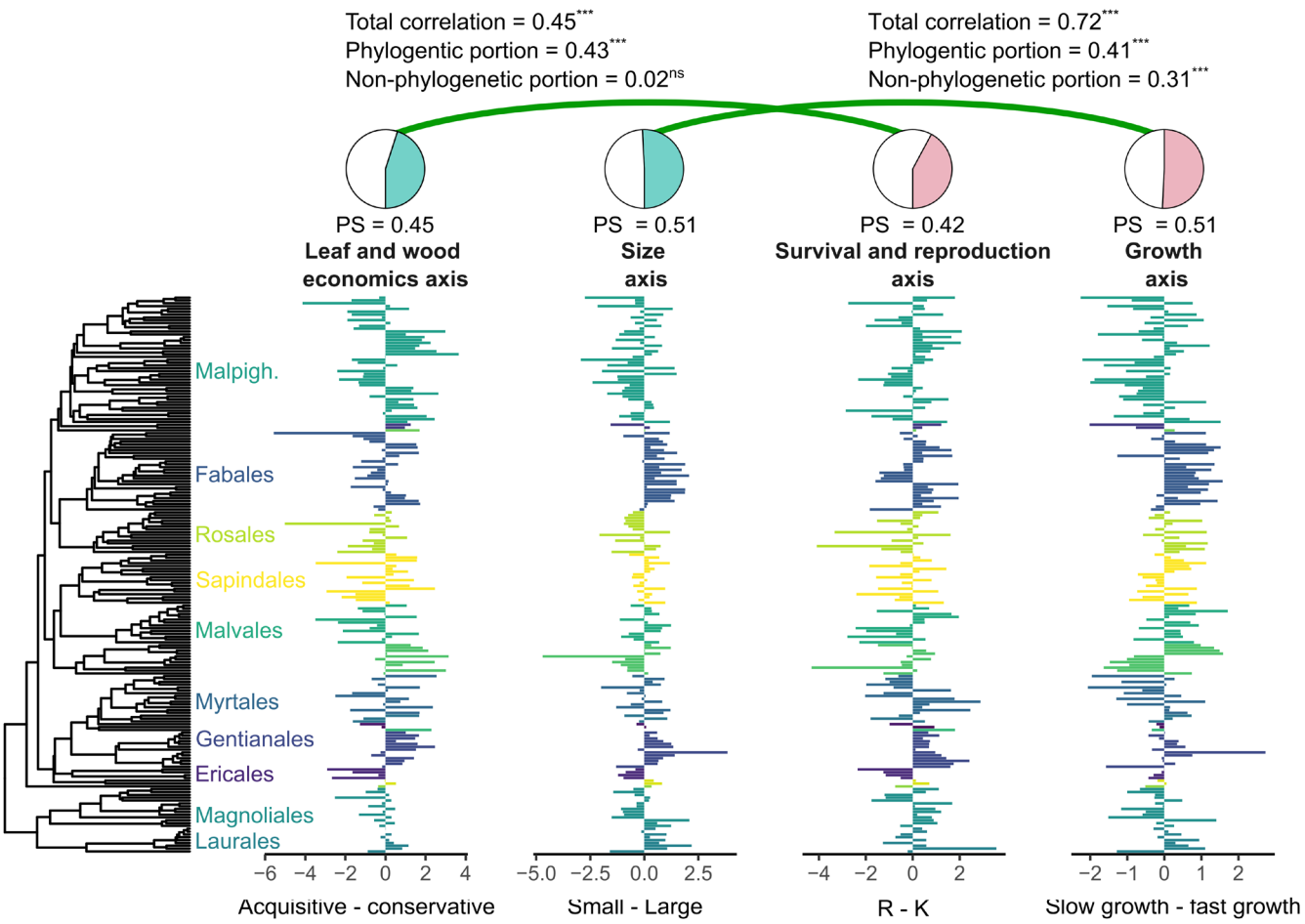

FIGURE 3 Functional and demographic axis correlations. Total, phylogenetically conserved and non-phylogenetically conserved correlation portions between functional and demographic principal components. Phylogenetic signal is also shown and represented as pie charts for each principal component. Values for genera with complete observations are plotted on the genus-level phylogeny. Bars are coloured by taxonomic order and the most important taxonomic order names are shown. Signif. codes: "***": $p < 0.001$; "ns": $p > 0.1$.

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the coordination between the leaf and the wood economics spectrum (Chave et al., 2009; Wright et al., 2004), which are aligned in turn with seed mass and mortality rates. This axis describes, at one end, how genera with relatively larger and/or thinner leaves with higher N and P content tend to have lower wood density, potentially related to a higher water transport capability, lower defence and/or higher vulnerability to disturbances such as strong winds (Chave et al., 2009). This combination of trait values represents an acquisitive strategy in leaf and wood functional traits. These genera also have a lower life expectancy and smaller seeds, the latter potentially leading to a higher total production of seeds per year and better colonization ability (Moles & Westoby, 2006). This combination of traits points to a prioritization of annual fecundity over survival, where fecundity is more strongly influencing mean fitness (Adler et al., 2014), and corresponds to the classic definition of an R strategy (MacArthur & Wilson, 1967; Pianka, 1970).

The opposite end of the first axis describes genera with smaller and/or thicker leaves and lower N and P contents, likely related to lower productivity and a higher leaf lifespan (Wright et al., 2004). These genera show higher wood density, potentially related to lower water transport capability but higher tolerance to hydraulic and mechanical stress, pathogens, and parasites (Chave et al., 2009). This combination of trait values represents a conservative strategy in leaf and wood functional traits. These genera also have longer lifespans, potentially emerging from a higher stress tolerance, while also presenting a higher investment per unit seed, potentially leading to a lower production of seeds and less frequent recruitment but with a higher probability of success (Moles & Westoby, 2006; Smith & Fretwell, 1974). This combination of traits points to a prioritization of survival over annual fecundity, with survival more strongly influencing mean fitness (Adler et al., 2014), characteristic of the classic K strategy (MacArthur & Wilson, 1967; Pianka, 1970) (Figure 1).

This first axis corresponds partially to the previously reported shade-tolerance and size axis (Turner, 2001), and to the fast-slow continuum (Stearns, 1999). However, we show that the fast (pioneer) to slow (stress-tolerant) continuum is largely decoupled from correlated characteristics of maximum growth rate and maximum size, which instead form a second integrative axis of variation, as reported in global analyses (Díaz et al., 2016). Genera with a high growth capability and faster growth tend to reach larger stature, independently of their resource-use strategy, lifespan, or reproductive strategy. At the other end of the axis, genera that grow more slowly tend to present smaller sizes (Figure 1). Functional traits related to leaf and wood economics (Chave et al., 2009; Wright et al., 2004) may be constraining life history traits related to survival and reproduction, while they are relatively independent of an axis related to size and growth at the genus level. It is worth noting however that we characterized size as maximum size (i.e., adult size), related to access to light in the reproductive stage, which even if shown to be related to seedling growth (Poorter, 2007), may have a weak relationship in some cases (Needham et al., 2022). We did not detect the independence of reproductive strategy from the fast-slow continuum as previously reported (Rüger et al., 2018; Salguero-Gómez et al., 2016). However, we acknowledge that the characterization of reproductive strategies in our study is limited to seed mass and may not be representing all its variability.

While tropical tree genera can occupy any portion of functional-demographic space along these two axes (Figure 1), it can be heuristically useful to broadly group genera based on 'end point' strategies related to resource uptake and use, stress tolerance, reproduction, survival, growth, and stature. The first group is characterized by an acquisitive R strategy with large size and fast growth and can be identified as the *large pioneer strategy* (e.g., *Ceiba*). The second group presents a conservative K strategy with a larger size and faster growth and can be identified as the *large stress-tolerant strategy* (e.g., *Manilkara*). The third group displays an acquisitive R strategy with a smaller size and relatively slower growth (in terms of diameter increments) and can be identified as a *small pioneer strategy* (e.g., *Quararibea*). Finally, the fourth group shows a conservative K strategy with a smaller size and slower growth and can be identified as a *small stress-tolerant strategy* (e.g., *Psidium*). Note that these groups represent extreme relationships as described by the two integrative principal components and that intermediate strategies are the most prevalent.

Analysing trait-to-trait relationships in a pairwise manner tends to support the main axes of variation that we have described, but also reveals substantial nuance in trait-to-trait relationships (Figure 2). For instance, these results show how the two integrative axes are connected by means of the positive correlation between growth rates and leaf nitrogen content, by a negative correlation between growth rates and wood density, and by the positive correlation between mortality and growth rates. Higher leaf nitrogen content is related to higher growth rates, which leads to lower wood density related to higher mortality rates, linking the fast-slow axis with growth. This is consistent with the tendency of pioneer strategies to present faster growth, even though our results show how this coordination is not strong.

4.2 | The coordination of leaf and wood function with survival and reproductive strategies is phylogenetically conserved, while the size-growth coordination shows a substantial element of evolutionarily lability

The coordination between resource uptake and use (leaf and wood economics), stress tolerance, reproduction, and survival was almost entirely phylogenetically structured. As a result, their covariation is conserved through evolutionary time leading to a pattern of phylogenetic conservatism that involves multiple functional and demographic components. Under this scenario, lineages may not be able to rapidly change their functional and demographic strategies related to reproduction and survival, evidenced by closely related species having similar strategies (Losos, 2008). This pattern likely emerges from conserved and slow adaptation in response to edapho-climatic drivers (Crisp & Cook, 2012), leading to a predominant effect of environmental filtering influencing the distribution of those strategies over environmental gradients (light, water, and nutrient availability

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gradients, amongst and within sites). As a result, phylogenetic position of genera is expected to be informative of resource economics, survival and reproductive strategies in Amazonian trees.

The coordination between size and growth has similar phylogenetic conservatism but also a substantial portion of its correlation showing evolutionary lability. This result suggests that the evolution of different maximum growth rates and maximum sizes is partially evolutionarily constrained but, on top of that, there is some variance that presents a correlated, but phylogenetically independent, pattern of change.

Overall, these results suggest that the distribution of leaf and wood economics, survival, and reproductive strategies has likely been constrained over deep evolutionary timescales in Amazonian trees. In contrast, changes in growth rates may allow Amazonian trees to adjust to different levels of resource availability, which may also affect maximum size. These traits are interconnected and their variability is determined by multiple processes, leading to a mixed pattern where evolutionary lability and phylogenetic conservatism coexist.

4.3 | The meaning of phylogenetic conservatism and evolutionary lability and in the coordination of plant function and demography

The quantification of Phylogenetic Signal in individual characteristics, such as functional traits, is a common application of phylogenetic comparative methods that helps compare the evolution of different characters (Ackerly, 2009; Freckleton et al., 2002; Losos, 2008). However, its capability to show how functional strategies are distributed or originate is limited, as these strategies often involve several traits related to different biological processes. Looking at the phylogenetic structure of trait correlations can help reveal how evolution drove the co-occurrence of different trait values, which in turn represent coordinated strategies, moving past the univariate perspective (Sanchez-Martinez et al., 2024; Westoby et al., 2023). We posit that quantifying the phylogenetic conservatism in trait correlations underlying life-history strategies can help in hypothesizing eco-evolutionary processes shaping them.

Phylogenetic correlation may appear as an effect of phenotypical and genetic common factors that constrain the evolution of multiple traits, leading to phylogenetic autocorrelation in trait syndromes. However, this phylogenetic conservatism in trait relationships could also result from a conserved pattern of adaptation (i.e., phylogenetic niche conservatism) (Sanchez-Martinez et al., 2020). In this case, even if a common underlying genotype or phenotype may not exist, specific trait values may tend to be selected under a given set of environmental conditions as they represent successful ecological strategies. This scenario, coupled with stabilizing selection may lead to a pattern whereby closely related taxa present similar strategies in response to similar environmental conditions (i.e., phylogenetic niche conservatism) (Crisp & Cook, 2012). For example, let us consider the pioneer strategy, which benefits from resource availability ensuring a fast resource uptake and use. This strategy may be selected against when resources are scarce, constraining the appearance of new variations in traits conforming it in descendant taxa. The stress-tolerant strategy may be similarly constrained to environments with a higher resource limitation, showing trait syndromes that are not able to uptake and use resources fast. Under stabilizing selection, these trait syndromes are expected to be maintained within lineages over evolutionary times. Therefore, ecological strategies under stabilizing selection are expected to strongly determine the persistence of taxa under different conditions, conforming to a pattern of phylogenetic niche conservatism.

Some correlations amongst traits appear to consistently have both phylogenetically conserved and non-phylogenetically conserved portions in Amazonian tree taxa, such as the correlation amongst specific leaf area, leaf N, and P content, or the correlation between size and growth rates. These trait relationships may present a hardwired integration potentially underlined by phenotypic and genetic causal effects. Therefore, these traits' variability and their covariation may be influenced by slow adaptation related to the general characterization of the species' ecological niche, while also being responsive to more recent variability in environmental conditions. A lower number of trait correlations appear only to have significant, non-phylogenetic portions. One important example is the correlation amongst size, growth, and mortality rates. These evolutionarily labile correlations indicate that large taxa with high mortality and high growth rates appeared multiple times in distantly related lineages. These evolutionarily labile strategies may be more able to change in response to recent environmental modifications happening on shorter evolutionary timescales. This variability can be detected as a small correlation between ancestor and descendant values, which can lead to a higher divergence in trait values in closely related taxa. These strategies may be more flexible, responding to environmental changes over shorter timescales, by, for instance, increasing growth rates when conditions are favourable, which will affect tree size.

4.4 | Caveats and future directions

The current study has some caveats, such as the use of a genus-level phylogeny and mean trait values for genera, which may be underestimating intra-generic functional and demographic diversity and phylogenetic structure. Genus-level data were used because of the high uncertainty in both species identification and species-level phylogenies in the tropics (Baker et al., 2017). Focusing on the genus-level allowed us to better elucidate the effects of deep evolutionary divergence in functional ecology. In the future, species-level analyses will further clarify whether these patterns are maintained and extend to more recent evolutionary timescales. In this regard, future studies characterizing the predictability of species values from genus means will be of great interest.

Our estimates of the Phylogenetic Signal may be prone to some bias related to the fact that we lack trait or DNA sequence data for

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many tree genera in the Amazon. Moreover, we did not use data from angiosperms with non-tree growth forms or environments outside the lowland tropical rainforest. However, previous studies have addressed this issue and reported that even if this may be true, Phylogenetic Signal metrics bring meaningful information (Molina-Venegas & Rodríguez, 2017). Moreover, in our case, we found similar patterns of phylogenetic conservatism in PCAs using the subset of genera for which we have complete trait data (197) as in pairwise analyses of individual traits where sample sizes often exceeded 400 genera.

We also included a limited set of functional traits and demographic characteristics, those which had wide data availability. A better characterization of functional strategies and demographic strategies will allow further elucidation of tropical trees' ecological strategies and their macroevolutionary patterns. Our results will need to be revisited once more functional and demographic data become available for Amazonian taxa. In this regard, the inclusion of hydraulic and photosynthetic traits will allow us to better understand the mechanistic link between resource uptake and use, stress tolerance, and demography (Tavares et al., 2023). Including more functional traits related to reproduction will also allow to better characterize different strategies that we may not have been able to represent in the current work. Finally, the inclusion of environmental data in future studies will help elucidate the adaptive meaning of the strategies described.

We acknowledge that functional traits and demography may act at different scales (i.e., individual physiology to population ecology) and selective pressures on them may differ. However, we believe that understanding the patterns of variation and covariation in these variables in different locations can help better understand the processes underlying their evolution. In this study, we use principal component analyses jointly with trait networks to describe general patterns in functional and demographic strategies while elucidating the deep nuance in the data and results. By doing so, we show for the first time, a pattern of phylogenetic conservatism in the coordination of leaf and wood economics spectra with demographic characteristics in Amazonian tree taxa. This pattern can be used to perform data imputation in tropical tree taxa, which can help with the data scarcity problem in highly diverse regions. These predictions would enable explanation of the geographical distribution of functional characteristics and assessment of climate change impacts on ecosystems but needs to be complemented by sampling efforts to assess whether these macroevolutionary patterns hold at the level of species and intra-generic clades.

AUTHOR CONTRIBUTIONS

Pablo Sanchez-Martinez, Kyle G. Dexter, Hans ter Steege and Freddie C. Draper designed the study; Pablo Sanchez-Martinez analysed the data and wrote the first draft of the manuscript with contributions from Kyle G. Dexter, Hans ter Steege and Freddie C. Draper. Chris Baraloto, Iêda Leão do Amaral, Luiz de Souza Coelho, Francisca Dionízia de Almeida Matos, Diógenes de Andrade Lima Filho, Rafael P. Salomão, Florian Wittmann, Carolina V. Castilho, Marcelo de Jesus Veiga Carim, Juan Ernesto Guevara, Oliver L. Phillips, William E. Magnusson, Daniel Sabatier, Juan David Cardenas Revilla, Jean-François Molino, Mariana Victória Irume, Maria Pires Martins, José Renan da Silva Guimarães, José Ferreira Ramos, Olaf S. Bánki, Maria Teresa Fernandez Piedade, Dairon Cárdenas López, Nigel C. A. Pitman, Layon O. Demarchi, Jochen Schöngart, Bruno Garcia Luize, Evlyn Márcia Moraes de Leão Novo, Percy Núñez Vargas, Thiago Sanna Freire Silva, Eduardo Martins Venticinque, Angelo Gilberto Manzatto, Neidiane Farias Costa Reis, John Terborgh, Katia Regina Casula, Euridice N. Honorio Coronado, Abel Monteagudo Mendoza, Juan Carlos Montero, Flávia R. C. Costa, Ted R. Feldpausch, Adriano Costa Quaresma, Nicolás Castaño Arboleda, Charles Eugene Zartman, Timothy J. Killeen, Beatriz S. Marimon, Ben Hur Marimon-Junior, Rodolfo Vasquez, Bonifacio Mostacedo, Rafael L. Assis, Dário Dantas do Amaral, Julien Engel, Hernán Castellanos, Marcelo Brilhante de Medeiros, Marcelo Fragomeni Simon, Ana Andrade, José Luís Camargo, William F. Laurance, Susan G. W. Laurance, Lorena Maniguaje Rincón, Juliana Schietti, Thaiane R. Sousa, Emanuelle de Sousa Farias, Maria Aparecida Lopes, José Leonardo Lima Magalhães, Henrique Eduardo Mendonça Nascimento, Helder Lima de Queiroz, Gerardo Aymard, Roel Brienen, Pablo R. Stevenson, Alejandro Araujo-Murakami, Bruno Barçante Ladvocat Cintra, Tim R. Baker, Yuri Oliveira Feitosa, Hugo F. Mogollón, Carlos A. Peres, Miles R. Silman, Leandro Valle Ferreira, José Rafael Lozada, James A. Comiskey, José Julio de Toledo, Gabriel Damasco, Nállarett Dávila, Roosevelt García-Villacorta, Aline Lopes, Alberto Vicentini, Fernando Cornejo Valverde, Alfonso Alonso, Luzmila Arroyo, Francisco Dallmeier, Vitor H. F. Gomes, David Neill, Maria Cristina Peñuela Mora, Janaína Costa Noronha, Daniel P. P. de Aguiar, Flávia Rodrigues Barbosa, Yennie K. Bredin, Rainiellen de Sá Carpanedo, Fernanda Antunes Carvalho, Fernanda Coelho de Souza, Kenneth J. Feeley, Rogerio Gribel, Torbjørn Haugaasen, Joseph E. Hawes, Marcelo Petratti Pansonato, John J. Pipoly, Marcos Ríos Paredes, Domingos de Jesus Rodrigues, Jos Barlow, Erika Berenguer, Izaias Brasil da Silva, Maria Julia Ferreira, Joice Ferreira, Paul V. A. Fine, Marcelino Carneiro Guedes, Carolina Levis, Juan Carlos Licona, Boris Eduardo Villa Zegarra, Vincent Antoine Vos, Carlos Cerón, Flávia Machado Durgante, Émile Fonty, Terry W. Henkel, John Ethan Householder, Isau Huamantupa-Chuquimaco, Marcos Silveira, Juliana Stropp, Raquel Thomas, Doug Daly, William Milliken, Guido Pardo Molina, Toby Pennington, Ima Célia Guimarães Vieira, Bianca Weiss Albuquerque, Wegliane Campelo, Alfredo Fuentes, Bente Klitgaard, José Luis Marcelo Pena, J. Sebastián Tello, Corine Vriesendorp, Jerome Chave, Anthony Di Fiore, Renato Richard Hilário, Luciana de Oliveira Pereira, Juan Fernando Phillips, Gonzalo Rivas-Torres, Tinde R. van Andel, Patricio von Hildebrand, William Balee, Edelcilio Marques Barbosa, Luiz Carlos de Matos Bonates, Hilda Paulette Dávila Doza, Ricardo Zárate Gómez, Therany Gonzales, George Pepe Gallardo Gonzales, Bruce Hoffman, André Braga Junqueira, Yadvinder Malhi, Ires Paula de Andrade Miranda, Linder Felipe Mozombite Pinto, Adriana Prieto, Agustín Rudas, Ademir R. Ruschel, Natalino Silva, César I. A. Vela, Stanford Zent, Egleé L. Zent, Angela Cano, Yrma Andreina Carrero Márquez, Diego

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CONFLICT OF INTEREST STATEMENT

All authors declare no conflict of interest.

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SUPPORTING INFORMATION

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

Figure S1. Integrative principal components using simplified list of traits.

Figure S2. Integrative PCA bootstrap results.

Figure S3. Phylogenetic PCA.

Figure S4. First and third integrative principal components.

Figure S5. Leaf and wood principal component analyses.

Figure S6. Correlation and phylogenetic signal.

Table S1. Phylogenetic-signal values for individual traits and principal components.

Table S2. Correlation results.

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