

## Research

### Resolving whole-plant economics from leaf, stem and root traits of 1467 Amazonian tree species

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It remains unclear how evolutionary and ecological processes have shaped the wide variety of plant life strategies, especially in highly diverse ecosystems like tropical forests. Some evidence suggests that species have diversified across a gradient of ecological strategies, with different plant tissues converging to optimize resource use across environmental gradients. Alternative hypotheses propose that species have diversified following independent selection on different tissues, resulting in a decoupling of trait syndromes across organs. To shed light on the subject, we assembled an unprecedented dataset combining 19 leaf, stem and root traits for 1467 tropical tree species inventoried across 71 0.1-ha plots spanning broad environmental gradients in French Guiana. Nearly 50% of the overall functional heterogeneity was expressed along four orthogonal dimensions, after accounting for phylogenetic dependences among species. The first dimension related to fine root functioning, while the second and third dimensions depicted two decoupled leaf economics spectra, and the fourth dimension encompassed a wood economics spectrum. Traits involved in orthogonal functional strategies, five leaf traits in particular but also trunk bark thickness, were consistently associated with a same gradient of soil texture and nutrient availability. Root traits did not show any significant association with edaphic variation, possibly because of the prevailing influence of other factors (mycorrhizal symbiosis, phylogenetic constraints). Our study emphasises the existence of multiple functional dimensions that allow tropical tree species to optimize their performance in a given environment, bringing new insights into the debate around the presence of a whole plant economic spectrum in tropical forest tree communities. It also emphasizes the key role that soil heterogeneity plays in shaping tree species assembly. The extent to which different organs are decoupled and respond to environmental gradients may also help to improve our predictions of species distribution changes in responses to habitat modification and environmental changes.

Keywords: determinants of plant community diversity and structure, environmental filtering, functional traits, Neotropical forests, plant economics, tree communities



## Introduction

Functional ecology has experienced a renaissance with recent advances via the implementation of large trait screening studies and database construction for both animals (Brousseau et al. 2018, Wong et al. 2018) and plants (Levine 2016, Jetz et al. 2016, Bjorkman et al. 2018). Regarding plants, trait-based approaches have been instrumental to improve our mechanistic understanding of species functional strategies (Wright et al. 2004, Chave et al. 2009), individual performance and fitness (Wright et al. 2010, Hérault et al. 2011, Poorter et al. 2018), species distributions along environmental gradients (Kraft et al. 2008, Fortunel et al. 2014a, Bruelheide et al. 2018, Lourenço Jr. et al. 2020), as well as species effects on ecosystem-level processes (Fortunel et al. 2009, Bardgett et al. 2014, Franklin et al. 2020).

Previous works have suggested the existence of a global pattern among the wide variety of plant life strategies existing across resource gradients and biomes, with strong coordination among economic traits reflecting the performance and fitness of species in a given environment (Freschet et al. 2010, Reich 2014, Díaz et al. 2016). The plant economics spectrum (PES) states that functional traits might be coordinated across plant organs to maximize fitness, such that cheap or expensive tissues consistently occur across leaves, stems and roots in response to resource availability (Wright et al. 2004, Reich 2014, de la Riva et al. 2016, Flores-Moreno et al. 2019). In addition, we might predict coordinated selection on traits from different tissues that are related to similar functions, such as hydraulic conductance of roots, stems and leaves (Kong et al. 2017, Shen et al. 2019). For example, previous work showed that coarse root traits are highly correlated with similar traits measured in branches (Fortunel et al. 2012, 2014b), supporting the idea of an integrated functional strategy across organs in an individual.

A second way by which a PES may occur is if environmental filtering constrains tissue variation across environmental gradients, resulting in converging trait syndromes along these gradients. An increasing number of studies have shown how the distributions of functional traits of leaves, stems and roots are filtered across gradients of soil fertility and climate (Fortunel et al. 2014a, Cadotte et al. 2015, Lourenço Jr et al. 2020). However, few studies have included a breadth of both soil and climate gradients with an integrated view of the plants to disentangle their effects on functional composition (Wigley et al. 2016, Borgy et al. 2017, Pérez-Ramos et al. 2017), especially in tropical forests (but see Tsujii et al. 2016).

Tropical forest tree communities represent ideal systems in which to test for different manifestations of a PES because they harbour thousands of coexisting species (ter Steege et al. 2013) with broad functional trait variation (Baraloto et al. 2012). In particular, the Amazon region is characterised by a mosaic of forest habitats varying in soil fertility, water retention and light availability, offering ideal conditions to investigate trait-environment associations. For instance, white-sand forests host a unique flora, with species adapted to nutrient-depleted conditions and frequent water stress (Fine and Baraloto 2016). The

transition from nutrient-poor white-sands to relatively more nutrient-rich terra firme and seasonally flooded forests generate strong turnover in functional composition of leaf and wood traits (Fortunel et al. 2014a, Vleminckx et al. 2018).

The attractive model of a single whole plant economics spectrum has been hindered by some evidence for decoupled economic strategies in temperate and tropical tree communities, with species exhibiting contrasting construction costs suggesting that resource allocation operates differently across organs (Baraloto et al. 2010, Fortunel et al. 2012, Valverde-Barrantes et al. 2015). For instance, tropical tree species with dense wood can bear tough, long-lived leaves, but also cheap, short-lived leaves (Baraloto et al. 2010, Fortunel et al. 2012). Moreover, temperate tree species exhibit fine root systems that are largely decoupled from aboveground tissues (Valverde-Barrantes et al. 2015, Kramer-Walter et al. 2016), though we lack information for tropical tree species.

To date, very few studies have investigated the role of fine root traits on species distribution (Zalamea et al. 2016) nor the integration of fine root traits along with coarse root, leaf and stem traits across any broad environmental gradients. This partly results from the difficulties to collect root material and the loose definition of function for root systems (McCormack et al. 2015, Weemstra et al. 2016). Nonetheless, recent efforts indicate that root tissues are as functionally diverse as their aboveground counterparts (Laliberté 2016, Iversen et al. 2017, Valverde-Barrantes et al. 2017). Moreover, rather than being strongly constrained by abiotic conditions, root traits seem over-dispersed along soil gradients. Instead, belowground acquisition strategies seem to be driven by limiting similarity processes (Luo et al. 2021).

Here we test the manifestation of a PES using an unprecedented dataset consisting of 1467 tropical tree species inventoried for their abundance over 71 plots distributed across four contrasted habitats in French Guiana (white-sand, terra firme, seasonally flooded and cloud forests), with 19 functional traits describing leaf, stem and root tissues. We address the following specific questions:

1. Are associations among traits consistent with 1) the presence of a single whole plant economics spectrum, showing high coordination of all traits across organs, or with 2) a decoupling of strategies associated to a single organ or a single function involving multiple organs? Here we expect that if plants are experiencing a strong functional trade-off, all species will converge towards a set of trait values that maximize their resource use economy, as predicted by the PES. If alternative selective pressures act on organs (or functions) independently, then we expect a decoupling of traits among organs (or functions) at the species level.
2. Is there a convergent filtering among functional dimensions across environmental gradients? Do traits representing different organs or functions respond differently to soil fertility and climate gradients? We expect that areas with stressful conditions (i.e. low fertility and low water retention in white-sand plots) will select in tandem traits that will maximize carbon economy (stress-tolerant syndromes) at the community level.

## Material and methods

### Study area

Tree species inventories were carried out in ten lowland and lower mountain sites covered by mature tropical moist forests across French Guiana (Fig. 1a), at the eastern edge of the Guiana shield. Mean annual rainfall (calculated over the 2010–2018 period) across inventory sites ranges between 2150 and 3700 mm and is distributed seasonally throughout the year (Gourlet-Fleury et al. 2004; Table 1), with a dry season occurring between August and November (monthly rainfall  $\leq 100$  mm) and usually more pronounced toward the interior of the continent. Mean annual temperature (2010–2018) oscillates around 25°C, with low seasonal variation, and averages at 22°C in a relatively higher site ( $> 500$  m a.s.l.) located at Mont Itoupé in the centre of French Guiana. Each of the ten inventory sites comprised two to 12 0.1-ha plots (71 plots in total), separated by at least 500 m, and located on contrasted habitats: 1) terra firme, 2) white-sand and 3) seasonally flooded forests. Additional details regarding the description of the study area are available in the Supporting information.

### Tree inventories

We used a modified version of the Gentry plots proposed by Phillips et al. (2003) and described in Baraloto et al. (2013), consisting of ten parallel transects of  $2 \times 50$  m departing perpendicularly every 20 m from a 200 m central transect, successively oriented in alternate directions, and delimiting an area of 1.9 ha. Within each transect, all stems with a circumference at 1.3 m above soil level  $> 8$  cm (corresponding to a DBH of ca 2.5 cm) were inventoried. Voucher specimens were collected at least once for each putative distinct species per plot in the field, plus additional vouchers for individuals that were not completely identified in the field. Duplicate vouchers are currently stored in reference collections of UMR EcoFoG (Kourou, French Guiana), UMR AMAP (Montpellier, France), and/or ICTB (Miami, USA). A list of species with their voucher reference is available in Supporting information. Our inventories resulted in a dataset comprising 13 736 trees belonging to 1467 species (excluding 25 palm and fern species for which we could not sample whole plant functional traits), 348 genera and 81 families, with an average of 79 species ( $\pm$  SD=28) per plot (additional details regarding tree diversity and climatic characteristics in each study site are provided in Table 1).

### Functional traits

We assembled a dataset of 19 functional traits for the 1467 tree species inventoried in our 71 plots, including 11 leaf traits, two stem traits, one coarse root trait and five fine root traits (Table 2). Details on trait measurement protocol are provided in the Supporting information. Trait values were obtained from a dataset comprising measurements from

tissue samples collected on 8345 individual trees belonging to 1625 species distributed in 371 genera, 78 families and 26 orders in the Rosidae, Asteridae and early eudicots (Supporting information). 5735 of these individuals (68.7%) corresponded to trees inventoried in our 71 plots and represented 783 out of the 1467 inventoried species (53.4%). Additional measurements were made on tissue samples collected, respectively, on 1746 and 858 individuals from the Brazilian Amazon (near Manaus) and Peru (representing, respectively, 248 and 541 species, among which 119 and 60 were also observed in French Guiana). We assumed that trait values for the Brazilian and Peruvian samples were representative of the species present in French Guiana (Ackerly 2003, Crisp and Cook 2012). We deem this assumption reasonable, based on positive and significant correlations (t-test of Pearson's product moment) of species mean trait values between French Guiana and the two outside regions (Brazil and Peru), for 12 out of 18 traits that could be compared (one trait could not be tested due to sampling limitations; details in the Supporting information).

Seven hundred and seventy-nine out of the 1467 species of our French Guiana inventories were represented in the matrix of 8345 individuals  $\times$  10 traits. We therefore added 688 lines (1467-779) of empty trait values, corresponding to the species that were not represented in the individuals matrix, therefore producing a matrix of 9033 individuals and 2313 species on which we performed trait imputations of missing trait values. The percentage of missing values in this trait matrix ranged between 34.96% for the leaf area up to 87.90% for the coarse root wood-specific gravity (see the Supporting information for details). Although the latter percentage was high, fine root traits were measured on species covering a wide phylogenetic range (31 families and 9 orders in the Asteridae, Rosidae and Magnoliidae), while previous studies have suggested that phylogenetic trait conservatism represents a major determinant of root functional traits (Valverde-Barrantes et al. 2017). Similarly, woody traits, which showed proportions of missing values that exceeded 65%, have shown strong conservatism (Chave et al. 2006).

To fill the missing trait values, we used the Bayesian hierarchical matrix factorization method (BHMF, Fazayeli et al. 2014), an imputation procedure based on both 1) covariations among traits and 2) trait information at higher taxonomic levels (species, genus, family, order, class), in a hierarchical way. The BHPMF method has been proved efficient in assessing missing trait values even with a percentage of missing values higher than 90%, providing that there is a good phylogenetic coverage and/or a sufficient number of traits measured among species (Schrodt et al. 2015). This was the case with our traits as they were measured on species covering a wide phylogenetic range, while there were on average  $11.3 \pm 4.0$  (standard deviation) traits measured per species. Prior to the imputations, outliers in the distribution of each trait were eliminated following Zuur et al. (2010) as the BHMF method is sensitive to extreme values, then traits were normalised (Box–Cox transformation) and standardised (z-score transformation). We then detrended each trait with

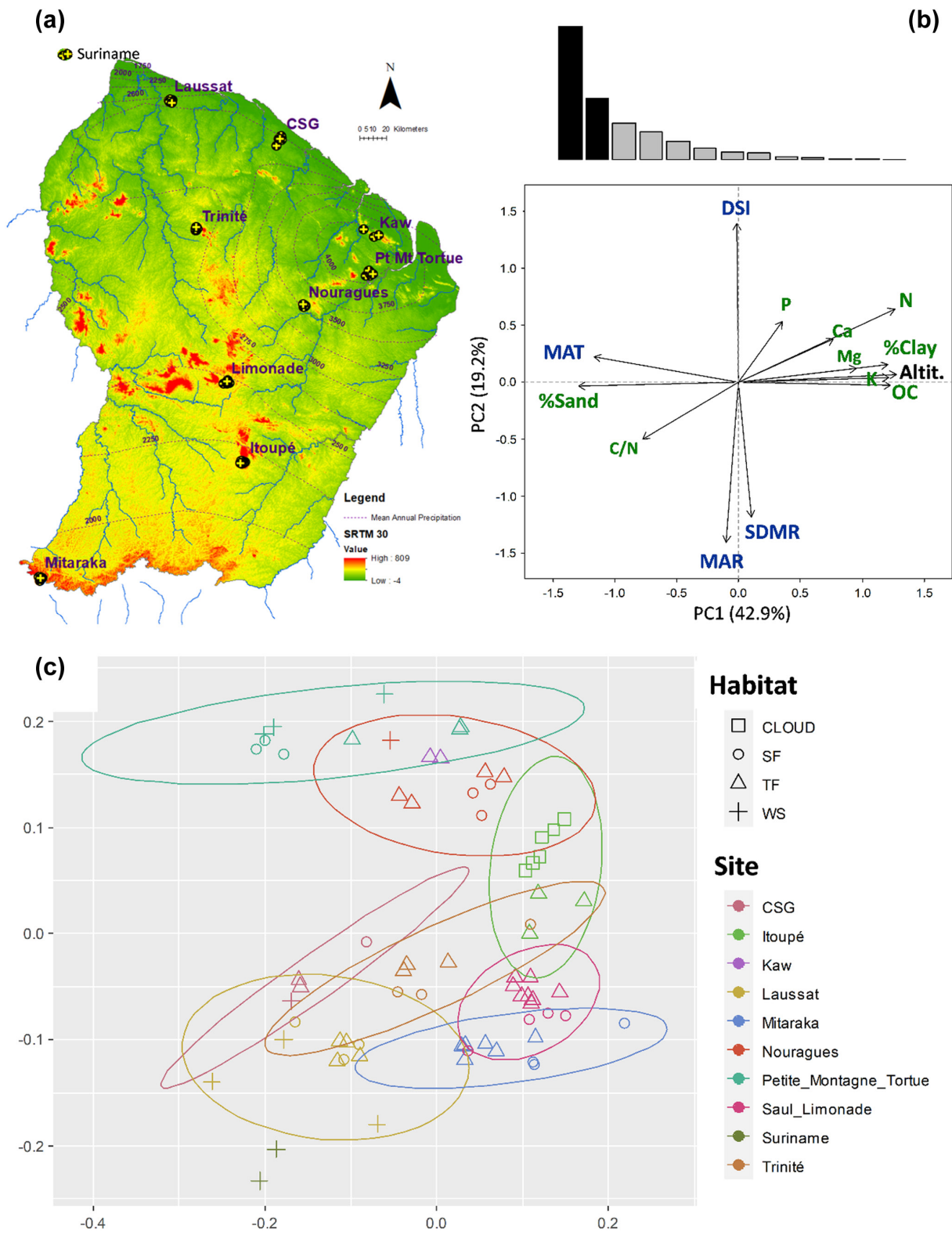


Figure 1. (a) Geographical distribution of the plots in the ten sites located in French Guiana and Suriname, and projection of (b) environmental variables (edaphic and climate variables in green and blue, respectively; altitude in black) and (c) plot scores on axes 1–2 (horizontal–vertical) of a principal component analysis performed on environmental data. Habitats are characterised with symbols (Cloud= cloud forest; SF=seasonally flooded; TF=terra Firme; WS=white-sand) in (c) are represented by symbols and sites by colours. Histograms represent the relative eigenvalues of the PCA axes. Ellipses delimitate a 95% confidence interval calculated from a bivariate normal distribution of the plot scores.

Table 1. Data overview of the ten study sites (rows 1–10, in alphabetic order) and the four habitats (last four rows, shaded in grey). ENS<sub>2</sub>: mean (calculated at the plot level) effective number of species calculated from 10 000 random sampling (with replacement) of two individuals. Numbers in parenthesis correspond to the standard error of the mean.

	Number of plots	Altitudinal range (m)	Mean annual rainfall (mm)	Mean annual temperature (°C)	Mean number of species per plot	ENS <sub>2</sub>
CSG	4	42–45	2921	25.79	72.75 (9.93)	26.37 (4.33)
Itoupé	9	521–819	2584	22.41	86.00 (5.88)	44.65 (8.75)
Kaw	2	254–282	3720	24.54	95.50 (6.50)	73.78 (18.57)
Laussat	10	49–57	2402	26.15	70.90 (3.27)	27.10 (3.39)
Mitaraka	9	317–355	2158	24.87	68.11 (10.63)	77.16 (17.55)
Nouragues	8	108–345	3328	24.82	85.63 (13.86)	72.63 (18.18)
Petite Mont. T.	9	47–136	3729	25.40	93.00 (10.59)	71.68 (15.56)
Saül-Limonade	12	196–253	2421	24.59	64.50 (4.22)	30.71 (3.84)
Suriname	2	39–58	2242	26.64	38.00 (4.00)	10.11 (6.31)
Trinité	6	126–320	2671	25.13	110.5 (11.89)	75.87 (14.18)
Cloud forest	6	577–819	2611	22.10	89.83 (8.19)	52.20 (11.84)
Seasonally flooded	20	45–347	2775	25.19	66.05 (4.86)	38.46 (4.28)
Terra firme	35	43–529	2723	24.92	90.37 (4.92)	68.55 (7.82)
White-sand	10	39–345	2909	25.71	59.00 (5.49)	20.90 (4.67)

the height of individuals to remove any ontogenetic variation effect, by regressing each trait on height and using the residuals of each regression as our trait values. Imputations were then calculated using the *GapFilling* function in the R *BHPMF* package (Fazayeli et al. 2014), using observed information available at the genus, family, order, subclass and class level to estimate missing trait values. We then extracted the imputed values at the individual level and calculated a matrix of mean trait values at the species level for the 1467 species of our French Guiana inventories. Post hoc analyses were carried out to evaluate the reliability of our imputations. These analyses showed that the whole correlation structure among traits was well preserved after imputation (Supporting information).

## Environmental data

Soil sampling and analyses were carried out using the protocol described in Baraloto et al. (2011). We collected ten bulked soil cores using 5 cm-diameter auger at 0–10, 10–20 and 20–30 cm depth in each plot, at each intersection between the ten parallel transects and the main central line. For each plot, the ten cores were then combined into a composite 500 g sample which was air-dried then sieved across 2 mm mesh and shipped all together for physicochemical characterisation at CIRAD soil lab (France) using standard soil analysis protocols (Pansu and Gautheyrou 2006). We retrieved nine soil variables, including two physical variables corresponding to soil texture (percentages of sand and clay), and seven chemical variables: soil organic carbon content, C:N ratio, available phosphorus (P), total soil nitrogen content (TN) and the availability of three base cations (Ca, Mg and K). The other variables used in our analyses comprised the elevation a.s.l. of each plot and three climatic variables calculated

using data extracted from <www.worldclim.org>, via the R package *raster* (Hijmans 2019): the mean annual rainfall (mm), the standard deviation of the mean monthly rainfall calculated over 12 months (to quantifies the unevenness of precipitation throughout the year). A dry season index (DSI) was also calculated for each site as the sum (over 12 months) of the ratios between mean monthly temperature and mean monthly rainfall to estimate of the potential water stress accumulated during the dry seasons.

## Data analyses

### *Plant economics strategies*

To address question 1 (is there a common economic arrangement among organs, consistent with a single PES, and how are different organs coordinated with each other?), we examined the functional heterogeneity among species using a principal component analysis (PCA). The PCA was used to examine correlations among traits from different organs, then identify whether 1) most of the functional variation was encompassed along a single dimension, with similar loadings among organs, or rather 2) whether different organs or any other trait assemblages explained independent and significant portions of the overall functional inertia. To take phylogenetic dependences among species into account, we compared this approach with a PCA performed using phylogenetic independent contrasts (Felsenstein 1985), a phylogenetic comparative method that converts the tips of the phylogeny of the 1467 French Guianan species into statistically independent objects. The ultrametric phylogenetic tree of these species was obtained using the *V.PhyloMakeR* package in R (Jin and Qian 2019). We scaled the branch lengths to one and calculated the phylogenetic independent contrasts as trait difference among pairs of sister species and nodes (Paradis et al. 2004). We then performed

Table 2. List of the 19 leaf, stem, coarse root and fine root traits and their mean values ( $\pm$  standard deviation) among species (species abundance not weighted;  $\pm$  standard deviation) in each habitat. Red and blue values indicate, respectively, the lowest and highest values among habitats for each trait. Asterisks indicate the significance of a one-way ANOVA testing trait mean differences among habitats (column 6) and of the Tukey tests of comparison for each habitat pair (columns 7–12). Tests were considered significant when the p-value was inferior to  $1 - (1 - \alpha)^N = 0.0027$  (Dunn–Šidák correction for multiple tests, with  $\alpha = 0.05$ , and  $n = 19$  is the number of traits tested). CL = cloud forest; SF = seasonally flooded; TF = terra firme; WS = white-sand.

	Cloud forest	Seasonally flooded	Terra firme	White-sand	ANOVA	SF-CL	TF-CL	WS-CL	TF-SF	WS-SF	WS-TF
<b>Leaves</b>											
Chlorophyll content ( $\mu\text{g mm}^{-2}$ )	67.82 (9.5)	69.32 (11.86)	69.47 (11.86)	71.35 (12.88)				*			
Thickness (mm)	0.22 (0.03)	0.22 (0.05)	0.22 (0.05)	0.27 (0.07)	*					*	*
Toughness ( $\text{N mm}^{-2}$ )	1.31 (0.32)	1.61 (0.45)	1.59 (0.5)	1.62 (0.55)							
Leaf area ( $\text{cm}^2$ )	69.93 (61.82)	78.59 (48.53)	71.65 (46.63)	60.0 (50.56)	*			*		*	*
SLA ( $\text{m}^2 \text{kg}^{-1}$ )	12.3 (3.47)	12.4 (3.18)	11.95 (2.77)	9.48 (3.01)				*			
C ( $\text{cg g}^{-1}$ )	47.24 (2.34)	47.86 (2.12)	47.99 (1.83)	48.55 (1.84)							
N ( $\text{cg g}^{-1}$ )	2.11 (0.41)	2.18 (0.49)	2.2 (0.51)	1.8 (0.42)	*					*	*
Leaf $^{13}\text{C}$ (‰)	-33.12 (1.12)	-32.6 (1.08)	-32.46 (1.11)	-32.56 (1.17)							
Ca ( $\mu\text{g g}^{-1}$ )	8062 (6466)	8784 (5581)	9260 (5503)	7293 (5007)							
P ( $\mu\text{g g}^{-1}$ )	744 (383)	830 (305)	808 (296)	556 (241)	*					*	*
K ( $\mu\text{g g}^{-1}$ )	7220.7 (4542)	8594 (3809)	8340 (3751)	6506 (2823)	*						
<b>Stems</b>											
Bark thickness (mm)	3.57 (0.77)	3.63 (1.48)	3.75 (2.01)	3.99 (1.12)							
Sapwood WSG ( $\text{g cm}^{-3}$ )	0.61 (0.08)	0.61 (0.1)	0.64 (0.1)	0.68 (0.11)	*					*	
<b>Coarse Roots</b>											
WSG ( $\text{g cm}^{-3}$ )	0.61 (0.14)	0.59 (0.16)	0.61 (0.17)	0.66 (0.14)							
<b>Fine Roots</b>											
Diameter (mm)	0.48 (0.16)	0.52 (0.12)	0.53 (0.12)	0.6 (0.17)	*						
Specific root length ( $\text{m g}^{-1}$ )	30.5 (31.46)	20.24 (18.07)	20.66 (18.22)	15.79 (10.97)							
Tissue density ( $\text{g cm}^{-3}$ )	0.34 (0.07)	0.38 (0.08)	0.4 (0.1)	0.39 (0.1)							
Specific root tip abundance (tips $\text{mg}^{-1}$ )	8.35 (10.6)	4.87 (4.89)	5.4 (6.19)	3.56 (3.61)							
Branching (tips $\text{cm}^{-1}$ )	2.71 (1.44)	2.49 (1.13)	2.59 (1.38)	2.07 (1.12)							

a Kaiser–Varimax rotation (Kaiser 1958) of the PCA axes in the spaces formed by axes 1–2 and axes 3–4, independently. This rotation maximises the association between the squared loadings of the traits and the principal components. This procedure allowed to better align traits with axes in our case, and so to interpret more easily the relationships among traits. The same approach was performed using the original imputed traits in order to identify any change of correlation structure when we do not take phylogeny into account.

### ***Environmental heterogeneity among plots***

Prior to addressing our second question which relates to how environmental conditions influence the composition of traits at the plot level, we analysed patterns of correlation among environmental variables and environmental differences among sites and habitats using a PCA performed on the 14 climatic and soil variables described above. We identified variables associated the most with the variation expressed along each PCA axis by calculating Pearson's correlations between plot scores on each axis and each environmental variable. We also tested the mean differences among habitats for each soil variable by using a one-way ANOVA test, followed by a Tukey test to compare differences among each habitat pair.

### ***Trait–environment associations***

Two complementary approaches were used to address question 2 (is there a convergent filtering among economics traits across environmental gradients, and do traits respond differently to soil fertility and climate gradients?): 1) a comparison of the mean functional trait values of species among habitats and 2) a more quantitative approach identifying traits significantly associated with soil fertility and climatic gradients.

The first approach consisted of testing the differences in mean trait values among species present in the four inventoried habitats (terra firme, seasonally flooded, white-sand and cloud forests), using a oneway ANOVA complemented by a Tukey test of comparison for each pair of habitats. The second approach aimed at examining in more details the pairwise associations between traits and environmental variables, using the fourth-corner analysis (FCA; Legendre et al. 1997). The FCA quantifies these associations by combining three matrices (a plot by environmental variables matrix, a plot by species abundance matrix and a species by traits matrix) into a single matrix quantifying trait–environment associations. Species abundances were Hellinger-transformed (Legendre and Gallagher 2001) to equilibrate the weight of abundant and rare species. To take spatial autocorrelation, as well as phylogenetic autocorrelation into account, the FCA statistic that quantifies the strength of trait–environment association (ter Braak 2017) was tested by comparing its observed values with 9999 null values obtained using a procedure based on Moran spectral randomisations (MSR, Wagner and Dray 2015) following Braga et al. (2018). The MSR method allows considering multiscale spatial and phylogenetic autocorrelation structures in any type of quantitative data. To do so, the method uses information on connectivity

among sampling points (i.e. the 71 plot in our case), which is obtained from the selection of Moran's eigenvector maps (MEMs, Dray et al. 2006). MEMs are commonly used to model multi-scale spatial structures in any type of numerical variable. The selection of MEMs was optimised following the procedure described in Bauman et al. (2018a, b) to take into account the nested pattern of our sampling design (using a Gabriel's graph to model connectivity among plots). The connectivity information is then used in a constrained randomisation algorithm in the MSR method to reproduce variables that accurately mimic the observed spatial structures of the randomised variable(s). The procedure is similar when taking phylogenetic autocorrelation into account, expect that phylogenetic eigenvectors are used instead of Moran's eigenvectors.

Values of the FCA association statistic were considered significant when they were lower than the 2.5th quantile (if negative) or higher than the 97.5th quantile (if positive) of null values. To avoid inflating the number of tests (14 environmental variables  $\times$  19 traits = 266 tests), we used plot scores from the first two axes of the PCA performed on environmental variables (explaining, 42.9 and 19.2% of the overall environmental inertia, respectively) instead of each environmental variable, as these axes were well interpretable and corresponded to a soil fertility gradient (axis 1) and a seasonality gradient (axis 2). This resulted in a reduced number of tests performed ( $n = 38$ ).

All analyses described in the methods were performed in R ver. 3.6.3 (<[www.r-project.org](http://www.r-project.org)>). The environmental, species abundance and trait data matrices, as well the R code and packages to reproduce all of our analyses are available in the Supporting information.

## **Results**

### **Environmental heterogeneity among plots**

The first axis of the environmental PCA (accounting for 42.9% of the overall environmental inertia) corresponded to a gradient of soil fertility opposing plots with high soil TN, K, Ca and Mg contents and % clay to plots with higher % sand and C:N ratio (Fig. 1). Plot scores on PCA axis 1 were the most highly correlated to soil TN and % sand ( $r = 0.93$  and  $-0.84$ , respectively; Supporting information). Most edaphic variation occurred within sites, with no marked differentiation of sites along the axis. Temperature also contributed substantially to the first axis, with decreasing temperatures highly associated with elevation and relatively fertile conditions.

The second axis (modelling 19.2% of the overall environmental heterogeneity) was most strongly associated to DSI ( $r = -0.90$ ), mean annual rainfall ( $r = 0.89$ ) and standard deviation of the mean monthly rainfall ( $r = 0.78$ ) (Supporting information), opposing sites receiving relatively high amounts of precipitation throughout the year (Petite Montagne Tortue, Nouragues, Kaw, Itoupé and Trinité) to sites with a relatively more pronounced seasonality (Centre Spatial Guyanais,

Laussat, Saül-Limonade, Suriname and Mitaraka). All soil variables differed among the four habitat types ( $p \leq 0.05$ , one-way ANOVA test; Table 3), with white-sand plots generally displaying lower soil fertility than the other three habitats (Table 3). Pearson correlations among all environmental variables are detailed in the Supporting information.

### Main functional dimensions and contribution of each organ to the overall functional variation

We will hereafter refer to ‘PCA’ and ‘PCA<sub>PIC</sub>’ to designate the PCA obtained using imputed trait values and the PCA obtained using phylogenetic independent contrasts (PIC), respectively, in order to facilitate the reading. Both PCAs produced significantly similar configurations of trait correlation patterns, as shown by highly significant values of the Procrustes statistic comparing trait projections on axes 1–2 (0.806) and 3–4 (0.599) (Fig. 2), suggesting a relatively low influence of species evolutionary history over the whole pattern of correlations among traits. Nevertheless, some particular trait associations substantially changed from one PCA to another, especially when projecting traits on axes 3 and 4.

Each of the first four dimensions in both PCAs expressed a variation that was higher than expected under a broken stick model (Jackson 1993), and higher than 99% of the variation expressed by these dimensions under null models that completely randomise trait values among species (i.e. assuming that all species could have evolved any trait value). We therefore characterise the traits and strategies most associated with the first four dimensions of these two PCAs. The Supporting information shows the contribution of each trait to the variation of each PCA axis and the correlations among traits, respectively.

The first dimension of the PCA (accounting for 23.9% of the overall functional inertia) and the PCA<sub>PIC</sub> (15.1%)

mainly depicted a variation in fine root morphology (Fig. 2), with fine root traits contributing for 75.6 and 79.1% of the dimension’s variation in the PCA and PCA<sub>PIC</sub>, respectively. This dimension opposed species with highly branched and thin roots to species with coarser fine roots (higher root diameter) and lower branchiness. Leaf C content also contributed substantially to the first axis’ variation in both PCAs (Supporting information), and was strongly associated with fine root diameter (r-Pearson=0.72 and 0.52 when using trait and PIC data, respectively; Supporting information).

The variation modelled by the second dimension (representing 16.3 and 11.5% of the whole variation in the PCA and PCA<sub>PIC</sub>, respectively) was mostly explained by leaf traits which contributed for 76.2 and 95.1% of the variation in the PCA and PCA<sub>PIC</sub>, respectively. In both PCAs, this second dimension reflected a leaf economics tradeoff opposing species with tough and thick leaves to relatively larger, softer, thinner and lighter leaves (higher SLA) with higher N content, and higher  $\delta^{13}\text{C}$  values in the PCA. In the PCA, leaf N content and SLA were also associated with high P and K contents, while thick and tough leaves were associated with dense fine roots and higher wood density in the sapwood and the coarse roots. In the PCA<sub>PIC</sub>, however, the three latter traits only weakly contributed to dimension 2, suggesting an influence of species evolutionary history on the correlations among these traits and with thickness and toughness, thereby explaining the difference (18.9%) between the two PCAs regarding the relative contribution of leaf traits along the second dimension.

The functional variation expressed along the third dimension of the PCA and the PCA<sub>PIC</sub> was also mostly explained by leaf traits which contributed for 86.8 and 78.6% of the variation in the two PCAs, respectively. In the PCA, the third dimension (10.5%) represented a leaf tradeoff opposing species

Table 3. Mean ( $\pm$  standard deviation) of each soil variable in each habitat (columns 2–5), and p-values of the one-way ANOVA tests of the habitat type effect (column 6; \* $p \leq 0.05$ ). Asterisks in the last six columns represent the significance of Tukey tests of comparison for each habitat pair. Tests were considered significant when the p-value was inferior to  $1 - (1 - \alpha)^N = 0.0057$  (Dunn–Šidák correction for multiple tests, with  $\alpha=0.05$ , and  $n=9$  is the number of variables tested). CL=cloud forest; SF=seasonally flooded; TF=terra firme; WS=white sand. Red and blue values indicate, respectively, the lowest and highest values among habitats for each soil variable.

	Cloud forest	Seasonally flooded	Terra firme	White-sand	ANOVA	SF-CL	TF-CL	WS-CL	TF-SF	WS-SF	WS-TF
% Clay	63.4 (17.1)	20.6 (17.72)	46.54 (22.73)	4.21 (5.04)	*	*		*	*	*	*
% Sand	19.77 (8.38)	64.53 (24.89)	42.87 (23.14)	92.27 (6.86)	*	*		*	*	*	*
OC (mg kg <sup>-1</sup> )	3.94 (0.92)	4.73 (4.48)	3.18 (1.52)	2.24 (2.97)	*			*		*	*
TN (mg kg <sup>-1</sup> )	3.11 (0.64)	2.29 (3.25)	1.61 (1.35)	0.17 (0.22)	*			*		*	*
C:N ratio	12.65 (0.39)	15 (4.04)	12.89 (1.47)	18.16 (7.1)	*						*
AP (mg kg <sup>-1</sup> )	1.76 (0.54)	10.78 (15.51)	4.98 (5.75)	3.67 (4.11)	*	*	*			*	
Ca (mg kg <sup>-1</sup> )	0.25 (0.14)	1.26 (2.37)	0.52 (1.01)	0.16 (0.17)	*					*	*
Mg (mg kg <sup>-1</sup> )	0.27 (0.07)	0.81 (0.92)	0.32 (0.31)	0.22 (0.24)	*					*	
K (mg kg <sup>-1</sup> )	0.1 (0.02)	0.13 (0.11)	0.1 (0.04)	0.05 (0.05)	*			*		*	*



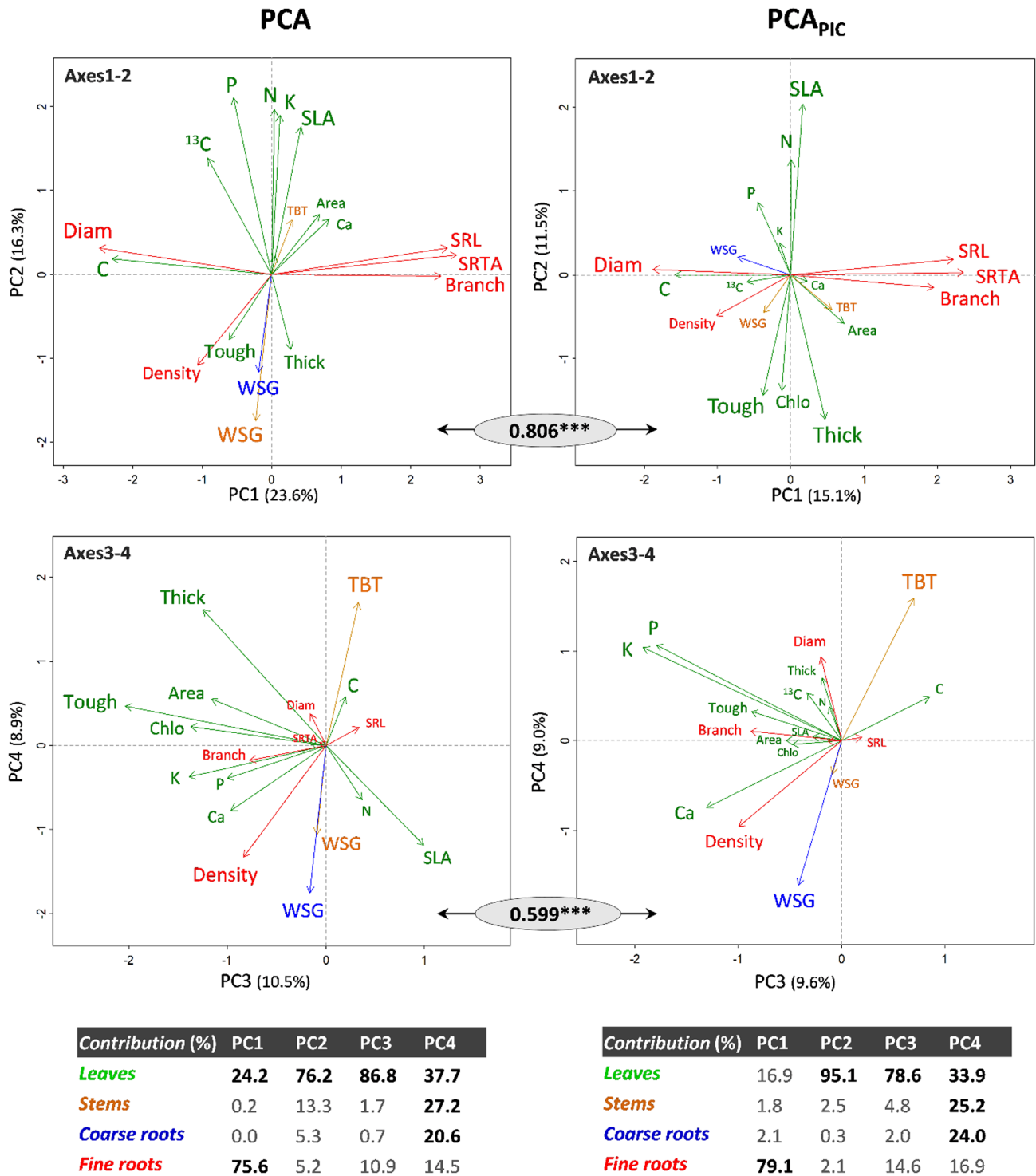


Figure 2. Projection of traits on axes 1–2 (above) and 3–4 (below) of a PCA performed on the matrix of 19 traits for the 1467 species inventoried in French Guiana, with trait data corresponding to either measured and imputed traits (PCA, left) or phylogenetic contrasts (PCA<sub>PIC</sub>, right). Leaf, stem, coarse root and fine root traits are emphasised with different colours shown in the bottom tables. The latter tables show the relative contribution of each organ (in%) to the inertia expressed by each axis, calculated for each organ as the sum of the squared trait loadings divided by the total sum of squared loadings among all traits. For each axis, the one to three organ(s) contributing for a total of at least 75% are emphasised in bold. Chlo=leaf chlorophyll content; Thick=leaf thickness; Tough=leaf toughness; Ca/K/P/N=leaf Ca/K/P/N content; Area=leaf area; WSG=wood-specific gravity of the trunk (orange) and the coarse roots (blue); TBT=trunk bark thickness; Branch=fine root branchiness; Diam=fine root diameter.

investing in thick, tough but large leaves containing high chlorophyll and nutrient amounts (Ca, K and P), to species producing softer leaves with higher SLA and lower nutrient amounts. In the PCA<sub>PIC</sub>, this third dimension (9.6%) was less influenced by leaf morphological traits (toughness, thickness, SLA and leaf area) but became mostly explained by a variation in leaf nutrient content, and opposed species containing relatively high versus low concentrations of P, K and Ca.

The fourth dimension of the PCA (8.9%) and the PCA<sub>PIC</sub> (9.0%) encompassed a stem economics spectrum, with stem and coarse root traits contributing for nearly 50% of the variation modelled by this dimension, with trunk bark thickness and coarse root wood density contributing the most among all traits (Supporting information). It formed a gradient of species with increasing wood density in the stems, which extended belowground with increasing coarse root wood density and fine root tissue density, and decreasing trunk bark thickness.

### Trait-environment associations

We found that species generally displayed more resource-conservation traits on poor soils, especially leaf traits (Fig. 3, Table 2). More specifically, two leaf traits reflecting resource capture strategies (leaf P and K contents) and two traits related to resource capture and defence (SLA and N content) showed relatively strong and significant positive association ( $p \leq 0.001$ ; test of the fourth-corner association statistic while taking spatial and phylogenetic autocorrelation into account) with the first axis of the environmental PCA. The latter modelled a fertility and temperature and elevation gradient, opposing plots located on lowland sandy and nutrient-depleted soils (negative scores along the axis) to plots occupying more fertile habitats at relatively higher elevation (positive scores) (Fig. 1b). At the same time, species with thicker leaves and thicker trunk bark, reflecting more resource conservation phenotypes, were significantly negatively associated with soil fertility. The significant associations in Fig. 3 were consistent with the results presented in Table 2, which shows that the nutrient-depleted white-sand habitat hosted species with more resource-conservation phenotypes (thicker and smaller leaves with lower N, P and K content) than in the other, more fertile habitats. Additionally, the same traits responding significantly to soil fertility in Fig. 3 showed fourth-corner association values  $> 0.24$  (leaf and bark thickness) and  $< 0.25$  (SLA and leaf N and P contents) with temperature (Supporting information).

White-sand plots were occupied by species with significantly denser sapwood (Table 2), although the correction of phylogenetic and spatial autocorrelation in the fourth-corner analysis did not show any soil fertility signal on wood density (Fig. 3). We found no significant associations between fine root traits and any environmental variables, neither between any traits and the rainfall-seasonality variation modelled by the second environmental PCA axis (Fig. 3). Nevertheless, fine root diameter was significantly higher in

white-sand soils than in other habitats (Table 2), although the ANOVA test did not correct for spatial and phylogenetic dependences.

From the fourth-corner results, we showed that traits that provided their highest relative contribution to orthogonal dimensions of the PCA and the PCA<sub>PIC</sub> (such as the trunk bark thickness and five leaf traits; Fig. 2) responded to the same fertility gradient across plots (as captured by the environmental PCA; Fig. 1b). The fourth-corner association values for all pairs of trait and environmental variable are detailed in the Supporting information.

## Discussion

Our study sheds light to the debate for the existence and the drivers of a whole plant economics spectrum (PES) in tropical tree communities, using an unprecedented dataset describing 19 leaf, stem and root traits for 1467 species in French Guiana, and a sampling design that covered a broad range of climatic and soil conditions at local (hundreds of meters) to regional (hundreds of kilometres) spatial scales, with plot-level replication of the main forest habitats. We found evidence for decoupled functional strategies among leaf, stem and fine root traits, with some leaf and stem traits involved in orthogonal functional dimensions ending up aligned along a soil fertility gradient.

### Four decoupled strategies among species, involving different organs and functions

Less than 24% of the overall functional heterogeneity was summarised along a single dimension (Fig. 2), thereby already showing that the variation of the 19 traits does not align along a single spectrum of fast versus slow strategies. This first dimension represented a tradeoff of fine root strategies stretching from highly branched root systems, potentially associated with acquisitive strategies, to thick roots and high leaf C content reflecting more resource conservation syndromes (Liese et al. 2017). The decoupling of fine root traits with other plant tissues is consistent with previous studies (Laughlin 2014, Laliberté 2016, Weemstra et al. 2016) and may suggest important differences in selective pressures in fine root systems with respect to aboveground organs. Several studies have stressed the importance of unique aspects in fine roots, such as the association with mycorrhizal symbionts and the presence of cortical tissues, that does not have a parallel adaptation in other plant organs, explaining the divergent variation of these tissues from other organs (Kong et al. 2019). The so-called ‘collaboration gradient’ described in Bergmann et al. (2020), emphasises the same tradeoff in fine root morphology that we observed along the first PCA and PCA<sub>PIC</sub> dimension (Fig 2). This tradeoff opposes species with thick roots and low specific root length (SRL) that outsource their nutrient via mycorrhizal symbioses, to non-symbiotic species producing highly branched root systems (high SRL), a pattern that was consistent across contrasted

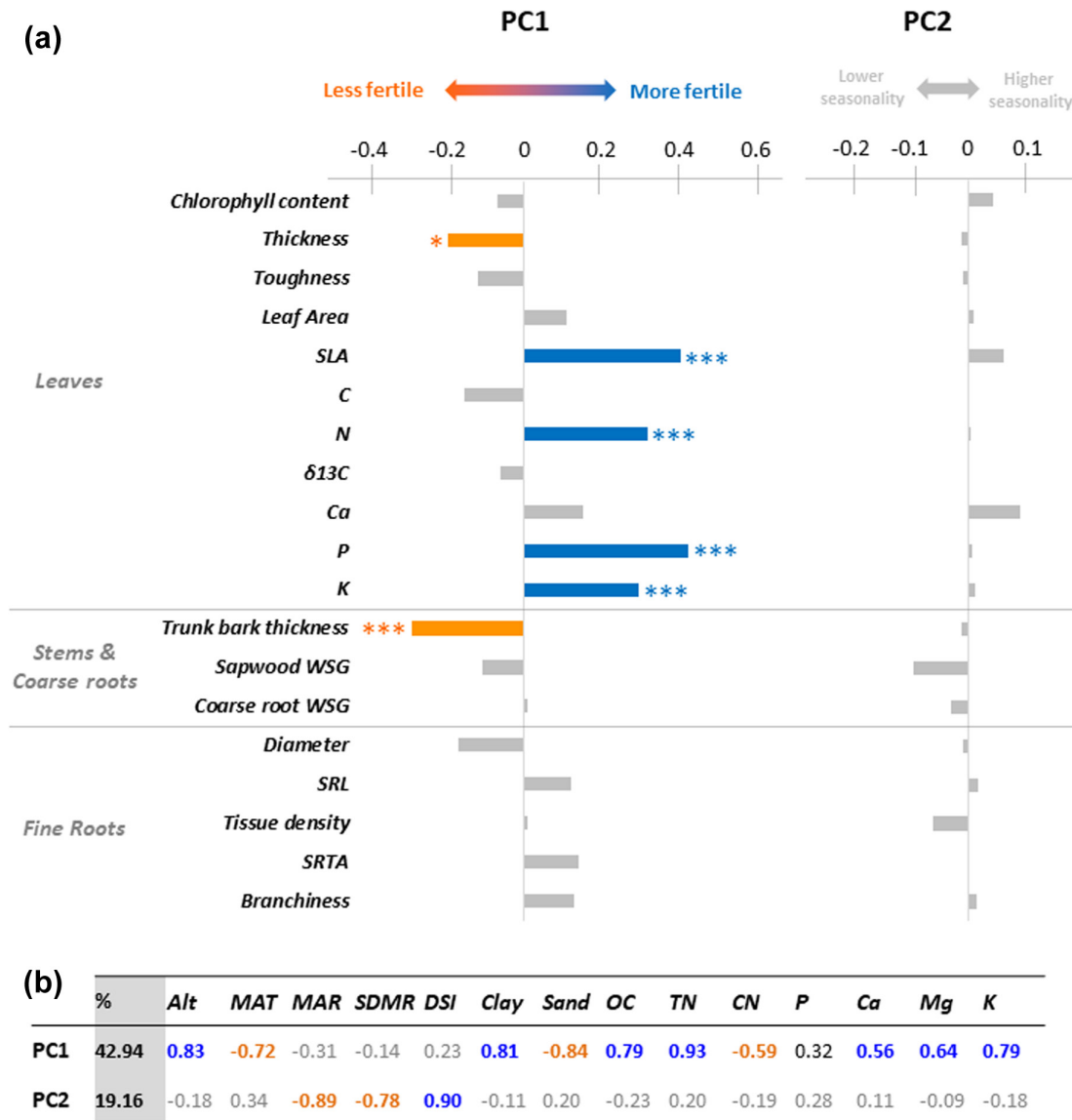


Figure 3. (a) Fourth-corner association values between leaf, stem, coarse root and fine root traits and the first two axes of the PCA performed on environmental variables, representing a soil fertility/acidity gradient and a rainfall/seasonality gradient, respectively (Fig. 1). Values were tested using the MSR method to correct for spatial and phylogenetic autocorrelation (with adjustment for the number of tests; 9999 randomisations). Significant values are represented with coloured histograms for clarity (positive in blue, negative in orange): \* $p \leq 0.05$ ; \*\* $p \leq 0.01$ ; \*\*\* $p \leq 0.001$ . (b) r-Pearson correlations between plots scores of the PCA performed on environmental data and each environmental variable. % = relative eigenvalue (in %) of each PCA axis. Correlation values  $>$  and  $<$  0.5 are coloured (positive in blue, negative in orange) to better identify the variables contributing the most to each axis.

biomes, including tropical forests (Bergmann et al. 2020). The authors also describe a decoupled variation in the fine root tissue density, as we did here, potentially depicting a fast–slow continuum related to soil fertility, although we found no significant association between fine root tissue density and soil conditions.

The second dimension of the PCA and the PCA<sub>pic</sub> showed a decoupled leaf economics gradient, supporting the result of previous studies carried out in tropical forests (Wright et al. 2004, Baraloto et al. 2010, Fortunel et al. 2012). This gradient opposed species with thin and large soft leaves (high

SLA) with relatively high N content, to species producing thick and tough leaves. This leaf economics spectrum was particularly well marked in the PCA<sub>pic</sub> where leaves contributed for 95.1% of the variation along the second dimension, whereas in the PCA, species with thick and tough leaves also displayed dense fine roots and dense wood in the stem and the coarse roots. The associations between the three later traits and leaf thickness and toughness may have thus resulted from the presence of conserved strategies coordinating these traits within certain clades, or because of a possible reinforcement of the phylogenetic signal during imputation for the traits that

contributed the most to the second dimension of the PCA. The latter explanation may explain why leaf  $\delta^{13}\text{C}$  contribution changed considerably between the PCA and the PCA<sub>PTC</sub>, as this trait presented relatively higher phylogenetic signal after imputation (Supporting information). While the leaf  $\delta^{13}\text{C}$  composition should in theory reflect the water-use efficiency, here this trait was positively associated with resource capture traits (SLA and leaf nutrient content) along dimension of the PCA. This trend seemed contradictory as we rather expected relatively higher  $\delta^{13}\text{C}$  values to be associated with resource-conservation traits (this is further discussed in the next section in light of our trait–environment association tests).

The third functional dimension also showed a continuum of leaf traits strategies, which in the PCA corresponded to species exhibiting low-to-high leaf mechanical resistance (tough leaves), leaf area and leaf micronutrient and chlorophyll content. In the PCA<sub>PTC</sub>, the third dimension mostly represented a tradeoff of leaf micronutrient content, with low contribution of morphological traits like toughness, revealing here as well the potential influence of conserved coordinated leaf morphological strategies along this axis or possible imputation-related reinforcement of the phylogenetic signal.

The fourth dimension corresponded for nearly 50% of its variation to a stem and root economics spectrum (Chave et al. 2009), along which species with thick trunk bark were opposed to species displaying denser wood and denser fine root tissue. The rhytidome (external part of the bark) provides a mechanical protection against physical damages and natural enemies (Paine et al. 2010). Our results may therefore suggest that species would either invest in thicker bark as a protection against physical and biological threats, or instead invest in denser wood that also confers protective and defensive functions (Cornwell et al. 2009), in addition to reduced cavitation risks (Santiago et al. 2004, Baraloto et al. 2010). These adaptations should therefore characterise species occupying either relatively less fertile soils (Fortunel et al. 2014a) and/or old-growth forests in which recruitment favours shade-tolerant species (Vleminckx et al. 2020). Dense-wooded species also displayed dense fine root tissues along the fourth dimension, possibly reflecting similar adaptations belowground (e.g. greater mechanical protection and lower cavitation risk) and the importance that the stele tissue in roots play in the total density of the tissue (Kong et al. 2019). The independent variation of fine root tissue density with other fine root traits (SRL, SRTA, branchiness, diameter) was consistent with previous findings (Kramer-Walter et al. 2016), reflecting the independence between tissue conservation and acquisition strategies in absorptive roots (Bergmann et al. 2020).

Our results together with consistent findings reported in the Amazon (Baraloto et al. 2010, Fortunel et al. 2012) suggest that species invest independently in leaf, stem and fine root tissues. These multiple functional dimensions across and within plant organs may have resulted from independent evolutionary histories or selective pressures shaping these traits, which contradict the hypothesis of a single plant economics spectrum (Reich 2014).

## Convergent response of decoupled leaf and stem traits to soil gradients

We found that five leaf traits (leaf thickness, SLA, leaf N, P and K content) and bark thickness, which contributed differently across independent functional dimensions were significantly associated to the same soil fertility and textural gradient (Fig. 3). Our results stand in line with previous studies in Amazonian forests showing that poor soil conditions select for species with conservative resource use strategies, likely to compensate for slow tissue turnover (Fine et al. 2006, Baraloto et al. 2010, Fortunel et al. 2014a). For instance, examining 15 aboveground and belowground traits across lowland Amazonian forest habitats, Fortunel et al. (2014a) found that tree communities displayed denser leaf, stem and woody root tissues on white-sand soils compared to more fertile habitats (Fig. 3). Our results also shed light on the importance of white-sand habitats in biodiversity conservation, as they host unique tree communities that exhibit stronger resilience to intensifying drought episodes in the eastern Amazon region (Marengo et al. 2012, Fine and Baraloto 2016).

Temperature, which also contributed substantially to the variation modelled by the first axis of the PCA performed on environmental data (Supporting information), showed significant positive associations (fourth-corner statistic = 0.24;  $p \leq 0.05$ ; Supporting information) with trunk bark thickness. However, we question whether the range of mean annual temperature observed across plots (22.4–26.6°C) may really influence bark thickness, and if so we lack hypothesis to explain it. Instead, we suspect the temperature signal to result from its strong covariation with soil fertility effect, the latter being more likely to select different bark thickness as different resource conservation or defensive strategies. At the same time, temperature was significantly negatively associated with SLA (−0.28) and leaf N (−0.25) and P content (−0.29) (Supporting information). These negative associations possibly resulted from similar covariation effects. Nonetheless, relatively cooler tropical temperature conditions, such as those encountered in cloud forests (> 600 m a.s.l. in French Guiana), are more likely to favour species producing larger and softer leaves that allow higher evapotranspiration levels.

Our data revealed no significant association between traits and the rainfall-seasonality gradient modelled by the second axis of the PCA performed on environmental variables (Fig. 3), despite previous works reporting strong evidence that gradient of annual rainfall, and/or seasonality induces a shift in the functional composition of forest tree communities in diverse ecosystems (Laughlin et al. 2011, Wiczyński et al. 2019, Anderegg et al. 2021), including tropical forests where hydraulics traits are greatly influenced by drought (Santiago et al. 2018, Gouveia Fontes et al. 2020). The lack of rainfall and seasonality signal in our study may likely result from the relatively narrow range of variation in these parameters among plots at the scale of our study (Table 1).

The fact that soil variables (and potentially temperature) had a relatively stronger effect than rainfall and seasonality was also partly explained by our study design which aimed at

capturing a high local soil heterogeneity. In particular, white-sand habitats displayed marked resource availability contrasts with terra firme and seasonally flooded soils (Table 3). Further studies integrating our dataset with other data covering broader gradients of seasonality and elevation would be useful to better examine how climate and soil jointly shape functional composition across spatial scales.

Leaves showed the strongest response to soil fertility/texture among studied organs, with five out of the 11 traits being significantly associated to soil fertility (Fig. 3). The greater sensitivity of leaf tissues to soil resource availability may be explained by the higher nutrient demands for the functioning of these organs. Species found on poor soils had more durable, resistant leaves, via thicker and tougher leaf tissues. Conversely, species on more nutrient-rich plots invested in thinner, softer and larger leaves (high SLA) to maximise light absorption (Shipley et al. 2005), or in higher leaf nutrient contents (in particular, P, K and N). Our results are consistent with previous work showing that tropical tree species on terra firme and seasonally-flooded habitats had higher leaf N content and SLA, and lower wood density than those occupying white sand habitats (Fortunel et al. 2014a).

We expected leaf  $\delta^{13}\text{C}$  to show higher values on well-drained sandy soils or with increasing seasonality (DSI), but this trait was not significantly associated to any environmental gradients (Fig. 3), nor was significantly different across habitats (Table 2). Thus, there may not be strong enough disparities in water deficiency across habitats and within the range of climatic conditions occurring in our sampling to detect a signal on this trait.

The sapwood density was positively although not significantly associated with poor sandy soils in the fourth-corner analyses (Fig. 3). Nevertheless, significant differences of wood density were observed between white-sand and other habitats (Table 2). These results were consistent with the prediction that wood density relates to growth rate. For instance, fast-growing, light-demanding trees are characterised by lighter wood than slow-growing, shade-tolerant trees (Plourde et al. 2015). Previous evidence has also suggested that the relative abundance of light-wooded, fast-growing tree species increases with soil fertility (Vleminckx et al. 2020).

Environmental associations were generally weaker with fine root traits. This result was in agreement with previous studies (Shen et al. 2019), and reflects the idea that roots can optimize resource acquisition with contrasting strategies under the same soil conditions, thus promoting niche segregation rather than convergence under filtering (Ostonen et al. 2007, Valverde-Barrantes et al. 2016). For instance, mycorrhizal dependency potentially relates to alternative morphologies related to resource acquisition but not necessarily to nutrient availability. In the case of tropical forests, the wide representation of phylogenetic groups may also influence the over-dispersion of traits across environments, since some traits are largely structured by relatedness (Valverde-Barrantes et al. 2017, 2020) and dominant tree families are evenly represented along environmental gradients. For instance, important families with contrasting

root systems like Lauraceae (thick roots, highly dependent on arbuscular mycorrhizal fungi) and Myrtaceae (thin roots occasionally associated with ectomycorrhizal fungi, Valverde-Barrantes et al. 2017) can be equally successful in similar habitats, suggesting that both strategies can be equally successful to acquire soil resources.

An important future direction will be the integration of demographic data describing performance and fitness, including survival, growth rates and seed production, which should be priorities for coordinated investment in tropical species. For example, higher wood density and lower specific leaf area have been found to correlate with increased survival rates (Kraft and Ackerly 2010, Poorter et al. 2018) and slower growth rates (Héroult et al. 2011, Rüger et al. 2012, Fortunel et al. 2016), suggesting a decoupling in traits between ephemeral tissues (i.e. leaf and finer roots) and structural organs (Baraloto et al. 2012). Previous studies have, however, suggested the existence of orthogonal strategies corresponding to a growth-survival tradeoff and a stature-recruitment tradeoff (Rüger et al. 2018). Thus, we might anticipate a decoupling of mechanical resistance in roots, stems and leaves due to different turnover rates and responses to different environmental factors (Fortunel et al. 2012, 2014a). We suggest that future studies work to integrate data on functional traits, species distributions and especially species performances across even broader environmental gradients than those studied here.

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## Author contributions

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**Claire Fortunel:** Conceptualization (equal); Data curation (lead); Formal analysis (supporting); Funding acquisition (supporting); Investigation (equal); Methodology (supporting); Project administration (supporting); Resources (lead); Supervision (supporting); Validation (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal).

**Oscar Valverde-Barrantes:** Conceptualization (equal); Data curation (lead); Formal analysis (supporting); Funding acquisition (supporting); Investigation (equal); Methodology (supporting); Project administration (supporting); Resources (lead); Supervision (supporting); Validation (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing

(equal). **C.s E. Timothy Paine**: Conceptualization (equal); Data curation (supporting); Funding acquisition (supporting); Investigation (supporting); Methodology (supporting); Project administration (supporting); Resources (equal); Validation (equal); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Julien Engel**: Data curation (lead); Funding acquisition (supporting); Investigation (supporting); Project administration (supporting); Resources (equal); Validation (supporting). **Pacal Petronelli**: Data curation (equal); Resources (equal). **Aurélien K. Dourdain**: Data curation (equal); Investigation (supporting); Resources (supporting); Visualization (supporting). **Juan Guevara** : Data curation (supporting); Investigation (supporting); Resources (supporting). **Solène Bérroujon**: Investigation (supporting); Resources (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Chris Baraloto**: Conceptualization (lead); Data curation (lead); Formal analysis (supporting); Funding acquisition (lead); Investigation (equal); Methodology (equal); Project administration (lead); Resources (lead); Software (supporting); Supervision (lead); Validation (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal).

## Data availability statement

The data supporting the results are available at Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.c59zw3r76>> (Vleminckx et al. 2021).

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