


















RESEARCH ARTICLE

Shifting trait coordination along a soil-moisture-nutrient gradient in tropical forests

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Abstract

1. Soil nutrients and water availability are strong drivers of tropical tree species distribution across scales. However, the physiological mechanisms underlying environmental filtering along these gradients remain incompletely understood. Previous studies mostly focused on univariate variation in structural traits, but a more integrative approach combining multiple physiological traits is needed to fully portray species functional strategies.
2. We measured nine leaf functional traits related to trees' resource capture and hydraulic strategies for 552 individuals belonging to 21 tropical tree species across an environmental gradient in Amazonian forests. Our sampling included generalist and specialist species from *terra firme* (TF) and seasonally flooded (SF) forests. We tested the influence of the topographic wetness index, a proxy for soil moisture and nutrient gradients, on each trait separately and on the trait integration through multivariate indices computed from the eigenvalues of a principal component analysis on the traits of the species. Finally, we evaluated intraspecific trait variability (ITV) for generalists and specialists by calculating the coefficient of variation for each trait.
3. Results showed that (1) the environment had a greater influence on trait syndromes than single trait variation. Moreover, (2) SF specialist species expressed a stronger leaf trait coordination than TF specialist species. Furthermore, (3) the ability of generalist species to occupy a broader range of environments was not

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reflected by a larger ITV than specialist species but by the capacity to change trait coordination across environments.

4. Our work highlights the need to investigate functional strategies as multidimensional syndromes in physiological trait space to fully understand and predict species distribution along environmental gradients.

KEYWORDS

intraspecific variability, leaf functional trait, local habitat, species strategies, trait syndrome, tropical tree species

1 | INTRODUCTION

For decades, ecologists have worked to uncover the distribution patterns of plant species (Grisebach, 1872; von Humboldt, 1849). These efforts have long relied on observations of plant presence and abundance along environmental gradients (Dufrêne & Legendre, 1997; Futuyma & Moreno, 1988). Through these studies, soil nutrients and water availability have been identified as strong drivers of plant species distributions across scales (Esquivel-Muelbert et al., 2017; Vleminckx et al., 2023). While some species are restricted to specific portions of these gradients (so-called specialist species), others are widely distributed (so-called generalist species; Dennis et al., 2011; Kassen, 2002). The use of functional traits has progressively paved the way towards a better understanding of the mechanisms underlying such distributions and specific strategies, leading to more generalized predictions (Cadotte et al., 2011; Estrada et al., 2016; Lavorel et al., 1997; Reich, 2014; Violle et al., 2007).

However, studies that have attempted to explain plant distribution in the light of functional traits have found mixed results, calling into question the relevance of this approach (Shipley et al., 2016). Some studies have identified trait-environment relationships, supporting the idea that environmental gradients act as selective pressures that filter plant trait values, favouring those that confer survival and reproductive advantages under specific conditions (Andersen et al., 2012; Cosme et al., 2017; Fortunel et al., 2014; Hayes et al., 2014; McDonald et al., 2003; Oliveira et al., 2019, 2021; Zuleta et al., 2022). Conversely, other studies report weak or no trait-environment relationships (Bruehlheide et al., 2018; Fortunel et al., 2019; Weemstra et al., 2023), and the prevalence of such negative results is likely underestimated due to publication bias (i.e. the file drawer problem, Rosenthal, 1979). More generally, the use of functional traits has been recently challenged because of their limitations in explaining ecological processes (Anderegg, 2023; Funk et al., 2017; Karst et al., 2023; McGill, 2015; Shipley et al., 2016). Three main points can explain the mixed results across studies.

First, many studies relied on univariate methods (i.e. studying traits taken one by one), even though plant performance results from a cascade of processes controlled by many traits and their interactions at the whole plant level. Therefore, multivariate approaches are needed to fully understand how traits combine to build species

strategies across environmental gradients (Fortunel et al., 2014; He et al., 2020). The covariation of functional traits has been extensively explored to characterize species strategies, focusing on leaf traits (LES, Wright et al., 2004), wood traits (Chave et al., 2009), root traits (Bergmann et al., 2020; Weemstra et al., 2016) or whole-plant traits (Reich, 2014; Díaz et al., 2016; Vleminckx et al., 2021). While several studies highlighted the independence of these trait dimensions in explaining local community assembly (Baraloto et al., 2010; Falster et al., 2017; Rüger et al., 2018), few have investigated how trait space dimensionality and patterns of correlation vary across environmental gradients (Delhay et al., 2020; Messier et al., 2016; Rosas et al., 2019). These studies tend to show greater trait covariances (or trait integration) for trees growing in stressed environments. Therefore, trait integration may be as important as trait variances or ranges for understanding species distribution and community structure (Dwyer & Laughlin, 2017).

Second, many studies restricted their analyses to traits that are only weak proxies of the processes underlying plant performance in local environments and species distributions across environmental gradients (Shipley et al., 2016). While the link between performance and structural traits is often context-dependent, physiological traits offer direct measurements of processes (Brodribb, 2017; Volaire et al., 2020). As an illustration, leaf structural traits such as leaf thickness, toughness or mass per area have been used as proxies of plant responses to water availability, but several studies reported the absence of a clear link with hydraulic traits (Bartlett et al., 2012; Maréchaux et al., 2020). Under limiting soil water resources, a low leaf minimal cuticular conductance (g_{\min} , Duursma et al., 2019), a negative leaf water potential at turgor loss point (TLP, Blackman et al., 2010; Zhu et al., 2018) and a high leaf saturated water content (LSWC, Blackman et al., 2019; Medeiros et al., 2019; Luo et al., 2021) can each help maintain leaf hydration status. Additionally, high major vein length density (MajVLA) would provide more numerous and alternate water pathways around potential embolized veins (Peng et al., 2022; Scoffoni et al., 2011). However, each of these pathways to cope with limited water availability, has no direct or mixed effects on structural traits. Similarly, leaf chemistry has been reported to vary along soil fertility gradients, although the underlying processes remain unclear. While leaf nitrogen content (N) and leaf phosphorus (P) content showed a more consistent and direct response to soil fertility gradients (Fortunel et al., 2014; Gong et al., 2020;

Laughlin et al., 2018; Peguero et al., 2023; Vleminckx et al., 2021), other element concentrations, such as potassium (K), which support key functions such as maintenance of cellular turgor, osmotic pressure and stomatal control (Sardans & Peñuelas, 2015), have been related to soil water content (Oliveira et al., 2004) and have been underexplored.

Third, previous studies have predominantly focused on trait means, but intraspecific trait variability (ITV) has been increasingly recognized as a key determinant of species niches and distributions (Albert et al., 2011; Clark, 2010; Girard-Tercieux et al., 2023; Violle et al., 2012; Westerland et al., 2021). This variability integrates both genetic variation, through local adaptation, and variation in trait expression within individuals, through phenotypic plasticity (Albert et al., 2011; Violle et al., 2012; Westerland et al., 2021). This allows individuals to express different trait values along environmental gradients (Jung et al., 2014). The concept of ITV has been suggested to explain species niche breadth (Albert et al., 2011; but see Fortunel et al., 2019), with generalist species exhibiting higher ITV compared to specialist species (Büchi & Vuilleumier, 2014; Westerland et al., 2021). Consequently, on the one hand, higher ITV would reflect the large palette of functional traits expressed by generalists to adapt to diverse resource conditions (Dennis et al., 2011; Futuyma & Moreno, 1988; Kassen, 2002). On the other hand, lower ITV would reflect the narrow set of suitable trait values expressed by specialist species to establish and persist in specific habitats (Enquist, 2010; Enquist et al., 2015).

In this paper, we overcame these three limitations and explored whether trait syndromes that combine water-related traits with chemical traits, and ITV, could provide a better understanding of tree species' strategies along soil-moisture-nutrient gradients. More specifically, we leveraged the natural gradient spanning from the dry and low nutrient plateaus (*terra firme*, TF) to the wet and nutrient-rich valleys (seasonally flooded forests, SF) of French Guyanese tropical forests. To this aim, we measured five leaf water-related traits (leaf water potential at turgor loss point, minimum cuticular conductance, saturated water content, stomatal density and venation density) and four leaf chemical traits (leaf carbon, nitrogen, phosphorus, potassium) in 552 individuals belonging to 21 tropical tree species, which included six generalist, nine SF specialist and six TF specialist species.

We hypothesized that:

1. Environmental filtering along the soil-moisture-nutrient gradient would result in trait syndrome shifts, rather than single trait variation.
2. Specialist species would express different strategies linked to water and nutrient resources according to their topographic position, with higher trait integration in dryer plateau soils.
3. Generalist species would exhibit higher ITV compared to specialist species, reflecting their adaptability across environments.

By addressing these hypotheses, our study seeks to advance the understanding of how environmental gradients shape functional

strategies in tropical tree species by providing deeper insights into their physiological mechanisms.

2 | MATERIALS AND METHODS

2.1 | Study sites

The study was conducted in French Guiana during the dry seasons of 2020 and 2021 in three forest sites (Kaw, Paracou, and BAFOG), all belonging to the Guyafor permanent plot network ([Guyafor network/Experimental Design—Paracou research station, a large scale forest disturbance experiment in Amazonia \(cirad.fr\)](https://guyafor.cirad.fr/)). As members of the UMR EcoFoG, we were granted access to these sites. Specific permissions were provided by the scientific coordinators of each site: Géraldine Derroire for Paracou (CIRAD) and Thierry Breton (Office National des Forêts) for BAFOG. Access to the Kaw plots was approved by the Réserve Naturelle Régionale Trésor, managed by Trésor Association, through a formal derogation issued by the Collectivité Territoriale de Guyane (CTG). Mean annual precipitation across sites follows a west–east gradient and equals 2357, 3102, and 3851 mm/year, for the Kaw, Paracou and BAFOG sites respectively. The tropical forest of the Guiana Shield is characterized by heterogeneous meso-topographic conditions with numerous small hills, distinguishing two main contrasting habitats, *terra firme* (TF) forests and seasonally flooded (SF) forests (Ferry et al., 2010). SF forests are characterized by low elevation and seasonal hydromorphic areas and account for 7% of the Amazon basin area, while TF forests are characterized by plateau forests, non-hydromorphic areas and cover three-thirds of the area. The pre-Cambrian rocks of the Guiana Shield have been exposed to weathering and erosion for over two billion years, which has produced oligotrophic soils (Flores et al., 2020; Grau et al., 2017; Soong et al., 2020). TF habitats display a high clay content (~47%, Baraloto et al., 2021) and have a high water drainage. SF habitats are located in the valleys and are characterized by relatively more fertile, sandier soils compared to TF habitats (Allié et al., 2015; Baraloto et al., 2021) and a higher phosphorus content (P_{olsen} TF 4.4 mg.kg⁻¹; P_{olsen} SF 8.0 mg.kg⁻¹; Allié et al., 2015; Ferry et al., 2010). Specific to SF forests, the water table is never observed to descend below 60 cm depth, often reaching the soil surface or surpassing it for at least two consecutive months each year (Baraloto et al., 2007; Ferry et al., 2010) during the rainy season. However, this habitat is distinct from varzea and igapó forests, which become inundated by several meters of water for an extended period of 4 to 10 months (Junk & Piedade, 2011; Prance, 1979). To discriminate the habitats using a continuous index, we calculated the topographic wetness index (TWI) using a 30 m-resolution digital elevation model and the function `r.topidx` from the GRASS GIS software with default parameters. The topographic wetness index is a widespread index used in hydrological analysis, which is defined as the ratio between the upstream contributing area and the drainage induced by the slope. This index

thus captures the potential for water accumulation of a given area (Mattivi et al., 2019) and represents a proxy for soil moisture availability (Kopecký et al., 2020), where a higher TWI represents a higher soil moisture availability. This index has been used in a variety of studies pertaining to species distribution (Besnard et al., 2013; Kopecký et al., 2020; Ray, 2016; Schmitt et al., 2021). Additionally, previous studies have found that this measure is well correlated to nutrient availability in French Guiana (Allié et al., 2015; Schmitt et al., 2021) and well separates TF and SF habitats in each forest sites (see Figure S1 in Supporting Information). Across the three forest sites and two habitats, we sampled a total of 552 individuals belonging to 21 tree species in the two habitats. More specifically, we sampled 145 trees in Kaw, 226 in Paracou and 181 in BAFOG, (detailed information is available in Figure S2, Tables S1 and S2).

2.2 | Determination of species' preferences

Species' preferences were determined based on Baraloto et al. (2021). The Dufrene and Legendre method (Dufrêne & Legendre, 1997) was used as a measure of habitat association for each species, while taking into account spatial auto-correlation with the Moran Spectral Randomization method (Wagner & Dray, 2015). This measure, named IndVal for Indicator Value, scales from 0 to 1 and integrates both the relative frequency of each species across plots in a given habitat and its relative abundance in each habitat. A high IndVal indicates that a species is both frequent and abundant in a specific habitat, illustrating a strong habitat preference. Therefore an IndVal of 1 signifies complete habitat association while an IndVal of 0 denotes no association with the habitat. Out of the 654 species identified from Baraloto et al. (2021), we selected the 5% highest IndVal values in each habitat to qualify species as specialists of a habitat (Table S3). This corresponded to a threshold of $\text{IndVal}_{\text{TF specialist}} \geq 0.259$ for TF specialists (Figure S3a) and $\text{IndVal}_{\text{SF specialist}} \geq 0.200$ for SF specialists (Figure S3b). Those with an equal or lower IndVal in both habitats were considered without any preference and therefore called

generalists (Figure S3c). While we sampled species characterized as specialists of either TF or SF forests, in their "preferred" habitat, generalist species were sampled in both habitats.

2.3 | Trait measurements

We chose to measure leaf traits on randomly selected individuals (Table S2, Figure S4 for raw data variation) with a diameter at breast height (i.e. 1.3m, DBH) within the species-specific 10th and 90th percentile, thus excluding unusually small or large trees. While traits can vary along ontogenetic trajectory (Barton, 2024), this was not the focus of our study, and our sampling aimed at minimizing the effect of ontogeny while covering a representative sample of individuals for each species. We checked however that individual size did not have a substantial effect on trait variation (Figure S5). For each tree, we assessed the Dawkins index (Alder, 1992), which indicates the light incidence on the crown of the sampled tree (Figures S6 and S7). For each selected tree, we sampled 10 leaves using a big shot (Youngentob et al., 2016). Each leaf was rapidly placed in hermetic plastic bags with wet papers to avoid drying, and stored in the dark in a cooler until processing at the lab in the afternoon.

To guarantee that measurements were carried out on healthy leaves, we assessed chlorophyll fluorescence with a fluorescence meter (Mini-PAM II, WALZ, Effeltrich, Germany), which measures the maximum quantum yield of photosystem II (F_v/F_m) (Maxwell & Johnson, 2000). To quantify F_v/F_m , leaves were dark-adapted for 30min with a dark leaf clip (DLC-8, WALZ), then exposed to a saturating pulse of $5000 \mu\text{mol.m}^{-2}.\text{s}^{-1}$ with a wavelength of 650nm for 0.8s. Only leaves with a F_v/F_m value above 0.65 were considered for the study (Zhorl et al., 2015).

On healthy leaves, we measured nine leaf functional traits (Table 1): leaf chemistry (carbon, nitrogen, potassium, phosphorus contents) as resource capture traits and leaf water-related traits: leaf saturated water content (LSWC, g.g^{-1}), leaf water potential at which leaf cells lose turgor (TLP, MPa), leaf minimum conductance (g_{\min} , $\text{mmol.m}^{-2}.\text{s}^{-1}$), major vein length density (MajVLA, cm.cm^{-2}), and stomatal density (SD, mm^{-2}).

TABLE 1 Leaf functional traits and linked mechanisms.

Trait	Abbreviation	Unit	Type	Mechanisms
Carbon content	C	%	Chemical	Resource capture and defence
Potassium content	K	g.kg^{-1}	Chemical	Resource capture and water-use efficiency
Phosphorus content	P	g.kg^{-1}	Chemical	Resource capture
Nitrogen content	N	%	Chemical	Resource capture & defence
Minimal conductance	g_{\min}	$\text{mmol.m}^{-2}.\text{s}^{-1}$	Water-related	Water loss
Turgor loss point	TLP	MPa	Water-related	Drought tolerance
Leaf saturated water content	LSWC	g.g^{-1}	Water-related	Water capacitance
Major vein length density	MajVLA	cm.cm^{-2}	Water & carbon related	Water, sugar and hormone transport; mechanical support
Stomatal density	SD	mm^{-2}	Water & carbon related	Carbon uptake and water status

2.3.1 | Leaf water-related traits

We calculated LSWC based on saturated and dry weights (Barrs & Weatherley, 1962), with a digital scale at a 0.0001 g precision (Mettler Toledo, Switzerland). We obtained saturated weights by rehydrating the leaves for 24 h in the dark and at low temperature (4°C), and dry weights by drying leaves for at least 72 h at 60°C (Sapes & Sala, 2021). To calculate TLP, we followed the method of Bartlett et al. (2012) whereby branches are rehydrated overnight in order to measure the leaf osmotic potential at full hydration using a vapour pressure osmometer (Vapro 5600, Wescor, Logan, UT), from which the TLP is computed through a mechanistic-based correlation. We determined g_{min} from the consecutive weight loss of desiccating leaves that were sealed with nail polish on cut petioles (Sack et al., 2011). We weighed the leaves at regular intervals, twice at 15-min intervals and then each 30 min during 3–4 h to obtain leaf drying curves. Leaves of tropical species lose water very rapidly so that the given time intervals were sufficient to assess minimum conductance (Levionnois et al., 2021). Air temperature and humidity were monitored and recorded at each weight measurement using a digital thermo-hygrometer (Fisherbrand™ Traceable™ Relative Humidity/Temperature Meters). The slope of the curve of weight loss versus time was estimated using only the linear part of the regression ($R^2 > 0.95$), suggesting maximal stomatal closure (Billon et al., 2020).

Major vein length per area (Major VLA) was determined as the sum of the length of 1°, 2° and 3° order of major veins by analysing images scanned at high resolution (1600 dpi; Epson perfection V 800; Epson America Inc., Long Beach, CA, USA) of fresh leaves with the ImageJ software (Schneider et al., 2012) according to the standard protocol (Sack et al., 2011). To measure the 3° order vein lengths, we partitioned the leaf into three parts (bottom, middle and top). We drew three rectangular boxes, spanning at least two 2° veins, while avoiding the midrib. We measured 3° vein lengths in each box, subtracted the amount of 2° veins included in the boxed area, and averaged out the three calculations to get the 3° vein length per area of the leaf.

Stomatal density was calculated through the recently developed python interface labelStoma (Casado-García et al., 2020) and calibrated to our tropical species. More specifically, stomatal impressions

were made using transparent nail polish on three randomly selected middle sections of the adaxial side of each fresh leaf per tree. When dry, stomatal imprints were peeled off and mounted on glass slides. Pictures were taken at ×200 or ×400 magnification using a light microscope (Olympus-BX 51, Japan); with camera (Kern ODC 832, 5.1 MP, Germany). For the following four species: *Virola surinamensis*, *Virola michelii*, *Licania membranacea*, *Carapa surinamensis* stomata density was too difficult to assess because of the high abundance of trichomes even after leaf-cleaning or -waxing attempts.

2.3.2 | Leaf chemistry

Leaf chemistry was measured in Nancy, France at ISC SILVATECH—Structural and functional analysis of tree and wood Facility (doi: 10.15454/1.5572400113627854E12). Elemental analysis of major elements carbon (C) and nitrogen (N) was performed according to the Dumas method. For major and trace elements, potassium (K) and phosphorus (P), samples were then analysed using ICP-AES (ICP-AES 720/725 Agilent).

2.4 | Replication statement

The key elements of replication and experimental design can be found in Table 2.

2.5 | Statistical analyses

Traits were sampled for 11 to 48 individuals per species, resulting in a total of 552 tree observations (Table S2). All traits were standardized and normalized using the natural logarithm of the absolute value of the trait, with the exception that the natural logarithm of the absolute value of TLP was multiplied by −1 to interpret results the same way as raw data. We used the 'VIM' package (v. 6.1.1) (Kowarik & Templ, 2016) to calculate the percentage of missing values for each variable and visualize the missing data patterns. All leaf traits, except stomatal density, had less than 5% individual missing values.

TABLE 2 Details of replication.

Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Individual	Species	552 individuals belonging to 21 tree species; 11 to 48 individuals per species
Species	Habitat preference	6 TF specialist species; 9 SF specialist species; 6 generalists species
Individual	Habitat preference	113 TF specialist individuals; 214 SF specialist individuals; 225 generalists individuals
Individual	Habitat	247 individual collected in TF; 305 individuals collected in SF

Missing values were imputed using the 'mice' package (v. 3.15.0) (van Buuren & Groothuis-Oudshoorn, 2011) at the individual level. The mice function of the 'mice' package creates different plausible datasets by iteratively predicting missing values based on the observed data. We specifically used the predictive mean matching method for imputation. The first imputed dataset was selected for further analysis. Stomatal density (SD) had 26% of missing values and was not considered for imputation and therefore for multi-trait analyses (as imputation requires consistent trait measurements for each tree). The individuals for which SD was not measured were well distributed between TF and SF specialists. To clarify the different levels used throughout the manuscript, an *individual* consisted of a tree; a *species* as multiple individuals; the *habitat of collect* referred to TF or SF habitat locations where the tree was sampled; *species preference* referred to the three categories (generalist, SF specialist, TF specialist); the *environment* referred to the combined influence of the TWI at the tree location and the specific environmental characteristics unique to each of the three forest sites where the tree was sampled (Kaw, BAFOG or Paracou).

2.5.1 | Single-trait variation analyses

To quantify trait variability and identify its main drivers, we conducted a variance component analysis for each trait separately. We decomposed the variance for each of the nine traits separately using the following linear mixed-effects model (equation 1). The model has two fixed effects, TWI and the forest site (i.e. Paracou, BAFOG, Kaw). We therefore considered the environment to be the combined effect of TWI at the tree location and the forest site variable where the tree individual was sampled, as the forest sites also capture other factors related to the habitat other than TWI (i.e. precipitation, temperature, soil texture). To account for non-independence among observations, the model also included a random species effect A_i ,

$$\text{Model: } Y_{isj} = \mu + \alpha \cdot \text{TWI}_{isj} + \beta_j + A_{is} + \varepsilon_{isj} \quad (1)$$

$$\varepsilon_{ijs} \sim N(0, \sigma^2), A_{is} \sim N(0, \sigma_s^2)$$

In Equation 1, Y_{isj} represents the \log_e -transformed trait value for the individual i of species s sampled in forest site j . μ represents the overall intercept. α represents the regression coefficient for the fixed effect of TWI. TWI_{isj} is the value of the continuous predictor variable for the individual i of species s sampled in forest site j . β_j represents the categorical predictor for the fixed effect of forest site. A_{is} represents the random effect of species s . ε_{isj} represents the residual error term. Equation 2 represents an alternative model with no environmental effects and including only the random species effect. The models were fitted using the *lme* function in the *nlme* package (Pinheiro et al., 2023) by maximizing the log-likelihood,

$$\text{Alternative model: } Y_{isj} = \mu + A_{is} + \varepsilon_{isj}, \quad (2)$$

$$\varepsilon_{ijs} \sim N(0, \sigma^2), A_{is} \sim N(0, \sigma_s^2)$$

Using these two models, we were able to partition the variance between the environment, the species, and the individuals (or residuals).

2.5.2 | Multi-trait variation analyses

To explore species' strategies (i.e. trait syndromes among species), we performed several multi-trait variation analyses. A principal component analysis (PCA) based on individual trees was used to evaluate the patterns of covariation between traits (i.e. standardized and normalized trait values). Additionally, to test if trait syndromes were explained by species' preferences (SF specialist, TF specialist or generalist) or habitat of collect (SF or TF habitat), we performed permutational multivariate analyses of variance (PERMANOVA) on coordinates of all individuals on the first two axes of the PCA with the function *adonis2* (vegan, v.2.6-4, Oksanen et al., 2022), followed by a pairwise comparison with the *pairwise.adonis* function (*pairwiseAdonis* v. 0.4, Arbizu, 2020). To further investigate pairwise trait dependencies, we computed correlation matrices using Spearman's method for each species preference category (Figure S11, Table S5).

To investigate how the leaf trait integration evolved along the TWI gradient for generalist and specialist individuals, we computed two multivariate trait integration (TI) indices as described in Delhaye et al. (2020) for two sub-datasets separately: (1) generalists and (2) specialists. For each sub-dataset, we partitioned the TWI gradient into the maximum possible number of classes while ensuring that each class had a sufficient number of individuals to perform PCAs ($n_{\text{class}} = 6$). The number of individuals per class ranged from 22 to 61 individuals. The 6th class covered a wider range of TWI to get sufficient individuals for the calculations in both cases. We then computed six separate PCAs for each class using all the traits, resulting in 12 PCAs for the specialists and the generalists datasets. The two TI indices were calculated for each 12 PCAs as: (a) TI_{range} —the range of the eigenvalues of each PCA (i.e. the difference between the eigenvalues of the first and of the last axis of each PCA) and (b) TI_{sd} —the standard deviation of the eigenvalues of each PCA (Delhaye et al., 2020),

$$\text{TI} = \frac{\text{TI}_{\text{obs}} - \text{mean TI}_{\text{null}}}{\text{SD TI}_{\text{null}}} \quad (3)$$

In Equation 3, TI_{obs} represents the observed value for one of the two indices (either range or standard deviation). We then created a null distribution of both indices by sampling 1000 random communities from the whole species pool, constraining species richness to be maintained at the same value as in the local community. The mean ($\text{mean TI}_{\text{null}}$) and standard deviation ($\text{SD TI}_{\text{null}}$) of the considered TI index (either range or standard deviation) across the 1000 null communities were calculated. We thus calculated the standardized effect size of both indices (TI) to avoid any bias due to the number of individuals in each category. Values of TI indices reflect the level of constraints on the multidimensional trait space. For high values

of TI, one or a few axes explain a large proportion of the variation in the trait values, meaning that the trait space is more constrained than for low values of TI. Another approach to the detection of trait coordination was also carried out using network analysis. As this alternative approach gave consistent results, we present it only in the Supporting Information (Appendix S1).

2.5.3 | Intraspecific trait variability

To evaluate intraspecific trait variability (ITV) of species, we calculated the coefficient of variation (CV) for each trait for each species preference category (generalist, TF specialist and SF specialist). Following Yang et al. (2020), we used Bao's estimator, which is best suited after a logarithm transformation.

We used R version 4.2.1 for all statistical analyses (R Core Team, 2020).

3 | RESULTS

3.1 | Contribution of the environment to single-trait variation

The variance partitioning showed that trait values were largely determined by the species identity, that is interspecific variability and the individual level, that is intraspecific variability (Figure 1). The species explained between 35% (Potassium) and 69% (SD) of the observed variation. The residual variance corresponding to the intraspecific variation explained between 25% (SD) and 58% (Potassium). Intraspecific variation was higher than interspecific variation for g_{min} , carbon, potassium and phosphorus. The environment explained very little of the variation: it was highest for g_{min} (11%) and potassium (7%) but even null for carbon. Nonetheless, we observed a significant effect of the forest site variable for all traits as shown in the model summary for each trait in Table S6.

3.2 | Traits covariation

Almost 50% of the variance in leaf trait values was explained by the first two axes of the PCA (Figure S8). All leaf chemical traits highly contributed to both axes, explaining most of the total trait variation. For the first axis, chemical traits (phosphorus, nitrogen and potassium) and LSWC, respectively contributed up to 29%, 20%, 16% and 17% (Figure S9). For the second axis, chemical traits (carbon, potassium) and TLP, respectively contributed up to 34%, 27% and 27% (Figure S9). Interestingly, MajVLA and g_{min} were not well represented by the first two dimensions but contributed to the third dimension, respectively, 49% and 46% (Figure S9). The third axis explained 13.5% of the variation, but did not segregate species preferences nor habitats of collect (Figure S10). The permutational manova testing for differences in trait covariation according to

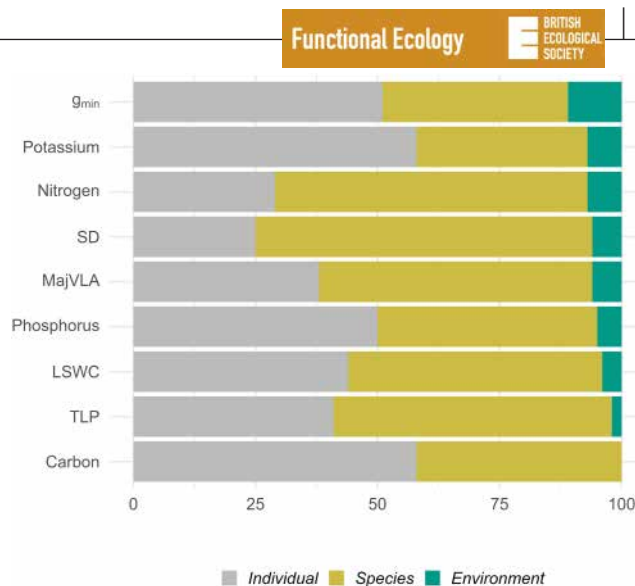


FIGURE 1 Variance partitioning of leaf traits across the environment, the species identity and the individual level. We decomposed the variance of each nine traits using a linear mixed-effect model that included a random effect for species (21 species). The environment combines both the continuous index of TWI and the categorical variable forest site (taking into account soil nutrient and water conditions across sites). Leaf traits, ordered by the contribution of the environment, from high to low: Minimum leaf conductance (g_{min} , $mmol.m^{-2}.s^{-1}$), potassium (Potassium, $g.kg^{-1}$), nitrogen (Nitrogen, %), stomatal density (SD, mm^{-2}), major vein density (MajVLA, $cm.cm^{-2}$), phosphorus (Phosphorus, $g.kg^{-1}$), leaf saturated water content (LSWC, $g.g^{-1}$), turgor loss point (TLP, MPa) and carbon (Carbon, %).

species' preferences revealed significant groups (Table S4a). We observed larger F-values for the pairwise post-hoc analyses between the SF specialists and generalists, indicating a more pronounced group separation than between TF specialist and generalists. The permutational manova on the habitat of collect, where the individual tree was sampled, revealed significant differences between the two habitats (Table S4b).

Pairwise correlation between chemical and water-related leaf traits (Figure S11, Table S5) showed varying patterns between species preference groups. For generalists, g_{min} and TLP were negatively correlated with potassium, while this was not the case for specialists. Weaker correlation coefficients were observed between water-related and chemical traits for SF specialists than for TF specialists. Concerning leaf chemical traits, the correlations between nitrogen, phosphorus and potassium showed strong similarity across all three groups of species preferences. We observed a particularly high significant correlation between nitrogen and phosphorus across all three groups of species preferences, highest for SF specialists ($r_s=0.76$, p -value<0.001) and lowest for generalists ($r_s=0.53$, p -value<0.001). The correlations involving Carbon had varying patterns across the three groups of species preferences. Concerning leaf water-related, neither strong nor significant correlation were revealed between water-related traits for generalists, except for the correlation between TLP and LSWC ($r_s=0.5$, p -value<0.001). Results showed that a greater number of water-related trait pairs

were significantly correlated for SF specialists compared to either generalists or TF specialists. Leaf minimum conductance (g_{\min}) showed a significant negative correlation with TLP ($r_s = -0.24$; p -value < 0.001) and a positive correlation with MajVLA ($r_s = 0.2$; p -value < 0.01) for SF specialists.

3.3 | Leaf trait syndrome variation along the TWI gradient

Both multivariate indices (Trait integration indices, TI) were calculated as the range and standard deviation of the eigenvalues of the PCA along the TWI and showed a strong increase towards the end of the TWI gradient, seasonally flooded soils (Figure 2). For generalist species, we observe a higher degree of trait coordination in both extreme ends of the TWI gradient (Figure 2a,b). For specialist species, the strength of the multivariate covariation between traits was higher for individuals sampled in seasonally flooded soils (i.e. SF specialists) than for individuals sampled in *terra firme* soils (i.e. TF specialists; Figure 2c,d).

3.4 | Intraspecific trait variability

Leaf traits showed non-negligible CV within species for all species preferences (Figure 3). The lowest CVs were observed for Carbon (0.9% for SF specialists; 1.1% for TF specialists and 1.3% for generalists) but also LSWC and SD. Moderate CVs were observed for TLP, MajVLA and potassium. The highest CV were observed for g_{\min} , with 68% for SF specialists, and 60% for TF specialists. Generalist species did not necessarily exhibit a higher CV compared to specialist species (Figure 3), but this was observed for potassium in seasonally flooded forests and some generalist species concerning nitrogen.

4 | DISCUSSION

Trait-environment relationships along environmental gradients has been extensively studied, revealing key mechanisms behind species community assembly and ecosystem functioning. However, previous studies have often focused on a limited set of commonly measured

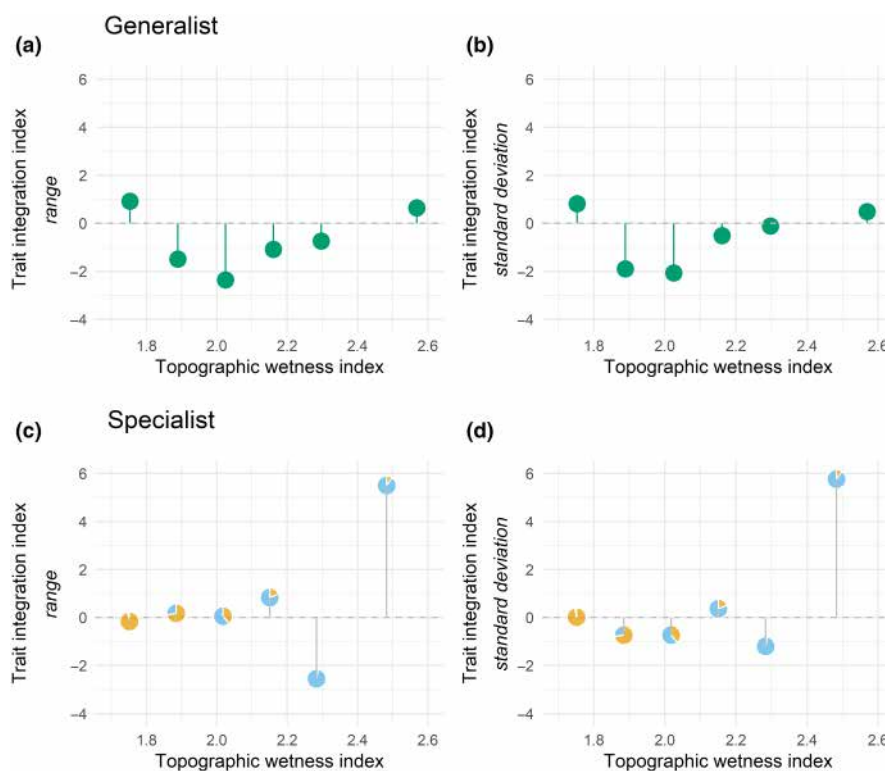


FIGURE 2 Variation of multivariate indices (Trait integration indices, TI) for (a, b, in green) generalist species and (c, d) specialist species, calculated as (a, c) the range and (b, d) the standard deviation of the eigenvalues of the PCA on eight leaf traits, along the topographic wetness index (TWI). Each point represents a group of individual trees belonging to the same TWI class. For (c and d), the colours indicate the respective proportions of TF specialist (orange) and SF specialist (blue). The proportion of TF:SF specialists along the gradient: Class 1 (0.97:0.03); class 2 (0.73:0.27); class 3 (0.39:0.61); class 4 (0.18:0.82); class 5 (0.03:0.97); class 6 (0.1:0.9). Terra firme habitats are characterized by low values of TWI and seasonally flooded habitats are characterized by high values of TWI. Leaf traits include: Carbon (Carbon, %), minimum leaf conductance (g_{\min} , $\text{mmol.m}^{-2}.\text{s}^{-1}$), potassium (Potassium, g.kg^{-1}), leaf saturated water content (LSWC, g.g^{-1}), major vein density (MajVLA, cm.cm^{-2}), nitrogen content (Nitrogen, %), phosphorus (Phosphorus, g.kg^{-1}) and turgor loss point (TLP, MPa). All variables were \log_e -transformed. TI > 0 represents an increase in trait coordination while TI < 0 represents a decrease in trait coordination.

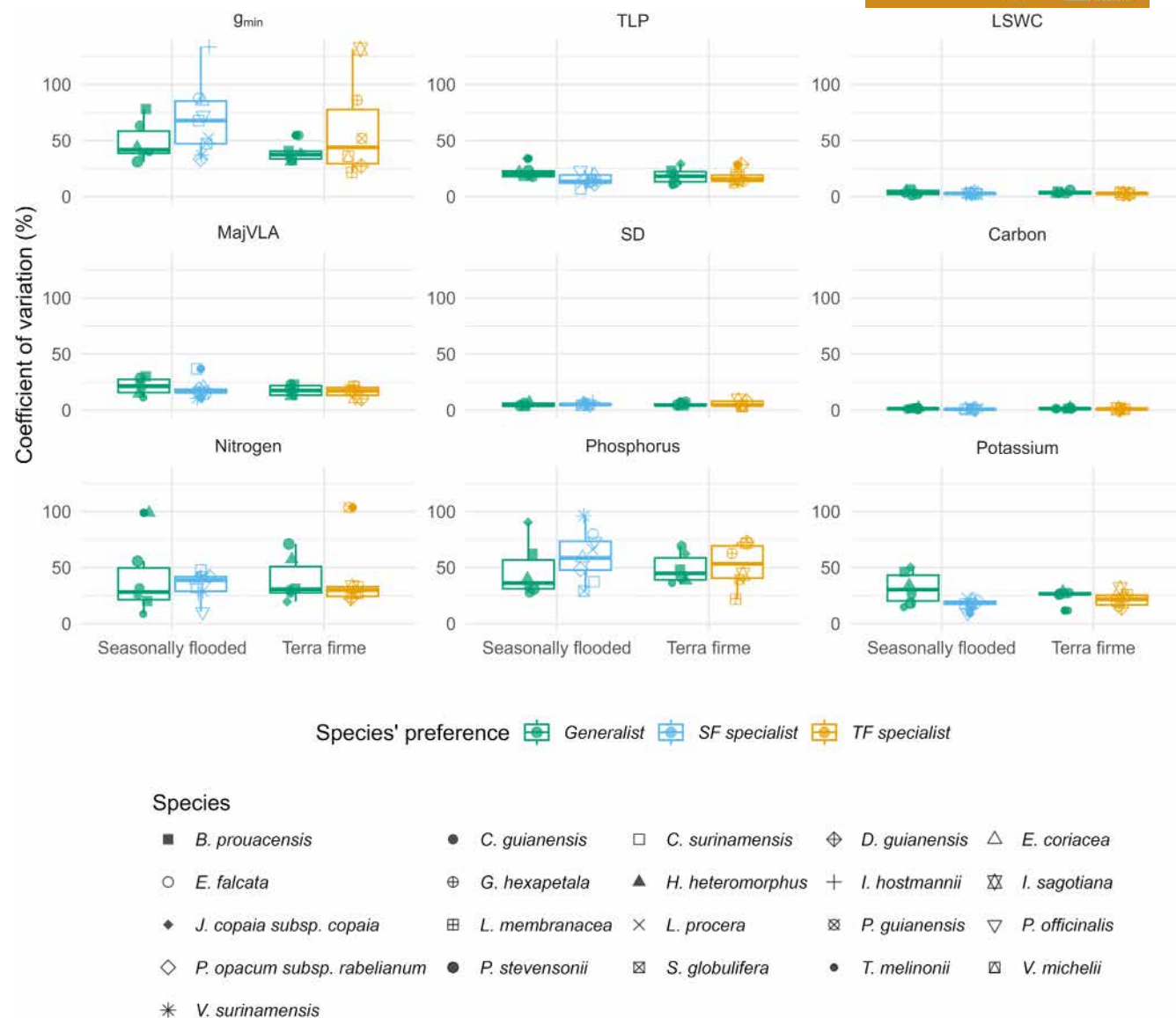


FIGURE 3 Coefficient of variation of individual tree trait values within species, given in percent, showing intraspecific variation for leaf traits across species per preference. A dot represents a species. Specialist species were only sampled according to their preferred habitat (TF or SF) and generalist species were sampled across the two contrasting habitats. Leaf traits include: Minimum leaf conductance (g_{min} , $\text{mmol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$), turgor loss point (TLP, MPa), leaf saturated water content (LSWC, $\text{g} \cdot \text{g}^{-1}$), major vein density (MajVLA, $\text{cm} \cdot \text{cm}^{-2}$), stomatal density (SD, mm^{-2}), carbon (Carbon, %), nitrogen (Nitrogen, %), phosphorus (Phosphorus, $\text{g} \cdot \text{kg}^{-1}$) and potassium (Potassium, $\text{g} \cdot \text{kg}^{-1}$).

structural traits and single trait variation along gradient approaches, overlooking the multidimensional nature of plant strategies. Using a large dataset of over 500 tropical trees, we explored leaf water-related and chemical traits along a soil-moisture-nutrient gradient using single and multi-trait approaches. First, we showed that the environment had a stronger influence on trait syndromes than single-trait variation. Second, we explored specialist strategies within *terra firme* and seasonally flooded forests and the later were revealed to be more constraining, with stronger leaf trait coordination with increasing waterlogging. Third, we showed that the ability to occupy a broader range of environments for generalists was not reflected by a larger intraspecific trait variability but by the capacity to change trait coordination across environments.

4.1 | Stronger environmental filtering when considering chemical and water-related traits collectively

Identifying the relationships between leaf traits and environment variables is crucial in understanding how environmental filtering shapes tree community composition. Our study underscores the minimal influence of the environment on single leaf trait variation (Figure 1). Although we found low explained variance, our results are consistent with Fortunel et al. (2020), who found that the habitat contributed to explaining chemical trait values (potassium, phosphorus and nitrogen) as well as stomatal conductance (light-statured in their case, g_{sat}). Their study reported higher explained

variance, which may be attributed to the inclusion of a third distinct habitat, white sands providing a greater and dryer, nutrient-poor contrast to TF and SF. In particular, our study reveals that the environment explained at best up to 7% for Potassium and 11% for g_{min} . Potassium is known to play a critical role in water economics (Sardans & Peñuelas, 2015), with high potassium concentration reducing water stress effects, since exported out of the cells, potassium enables stomata closure (Mohd Zain & Ismail, 2016; Santos et al., 2021) or alleviates waterlogging stress (Wang et al., 2013). Whereas it is still not clear how environmental factors can influence g_{min} (Duursma et al., 2019; Slot et al., 2021), differences found along the soil-moisture-nutrient gradient in this study, with higher g_{min} in dryer habitat TF and dryer site Bafog (Table S6), illustrates that soil water availability can drive trait variation. Moreover, we found limited effects of the environment on SD, and we suggest that future work on anatomical measurements and chemical composition of cuticular waxes should investigate whether environmental influences on water leakage are primarily due to leaf cuticle properties rather than stomatal properties (Figure 1). This could have important consequences when assessing water stress tolerance for tropical tree species and can help better predict how species could respond to environmental changes such as drought. Overall, the main drivers to single trait variation remain individual and species identity (Figure 1), as highlighted by previous studies (Fortunel et al., 2020; Rosas et al., 2019; Zuleta et al., 2022), rather than the role of the environment.

Covariation patterns among functional traits have been extensively studied across species and ecosystems (Díaz et al., 2016; Dwyer & Laughlin, 2017; Messier et al., 2017; Reich, 2014; Wright et al., 2004). Here, we found that leaf traits were more responsive to environmental factors when considered together (Figure S8; Figure 2). Although the multivariate space presents large overlapping of individuals of different species preferences and habitats of collect (Figure S8), the permutational manova reveals significant groups (Table S4). The soil-moisture-nutrient-gradient influences the strength of the relationship between chemical and water-related traits (Figure 2, Appendix S1). The level of trait integration has been recently used to investigate variation in multidimensional functional niche of species along environmental gradients, as it indicates how multiple traits covary (Delhaye et al., 2020). Stronger trait integration was found at the extremes of the gradient concerning generalist species (Figure 2a,b), and in the lowest point of seasonally flooded forests (TWI class 6) for specialist species (Figure 2c,d), as consistently shown by the two indices (the range and standard deviation). Previous studies have found higher trait integration in more stressful environments (Delhaye et al., 2020; Dwyer & Laughlin, 2017; He et al., 2021), indicating that species must coordinate their traits to optimize their resistance. Our results are consistent with these findings as generalist species at either end of the gradient and SF specialist species accommodate specific functional designs and a narrow range of trait combinations. These results highlight the importance of a more integrative approach combining multiple physiological traits to fully

understand the variety of tropical tree species strategies. As we assessed species' strategies along a soil-moisture-nutrient gradient, we only tackled two dimensions of the species' ecological niche. Other resources such as light might become limiting and could affect trait values (Figures S6 and S7; only marginally for the major vein length density). Future studies could simultaneously take into account water, nutrient and light dimensions of tree species niches, to complete our understanding of environmental filtering on trait syndromes.

4.2 | Seasonally flooded forests are harsher habitats than *terra firme*

Seasonally flooded (SF) and *terra firme* (TF) forest habitats mainly differ in terms of soil moisture and nutrients. How plants manage water, nutrient availability and potentially resist drought stress were highlighted to be essential to discriminate Amazonian species' habitat associations (Esquivel-Muelbert et al., 2017; Oliveira et al., 2019, 2021; Trueba et al., 2016) and have been shown to play a key role in niche specialization (Bittencourt et al., 2022). In this study, we specifically examined the link between species preferences (TF or SF specialists) and leaf chemical and water-related traits. We hypothesized that leaf water-related traits of TF specialists would be more constrained compared to SF specialists because TF habitats have dryer, better drained-soils, especially during the dry season. However, we observed (Figure S4) that the most negative turgor loss point values can be expressed by either TF (*L. membranacea*) and SF specialists (*P. opacum*), indicating that these species can resist leaf dehydration in either habitat, confirming previous results (Kunert et al., 2021).

Moreover, both multivariate trait integration indices (the range and standard deviation) revealed that the leaf trait syndrome was not constrained for the studied species until $TWI = 2.3$, which corresponds to seasonally flooded habitats (Figure 2c,d, Figure S1). A higher trait integration reflects a harsher environment that constrains leaf chemical and water-related traits together. Waterlogged soils are known to be very stressful but trees such as SF specialists, have developed multiple adaptations to persist in such environments (Parolin, 2001, 2010). We do note a lower trait integration for TWI in class 5 for SF specialists (Figure 2b) compared to the lowest point of seasonally flooded forests (TWI class 6). We could interpret this lower value in class 5 as SF specialists are best adapted to this level of waterlogging (low to moderate waterlogging). However, beyond a certain threshold of waterlogging (class 6), trees have difficulty to adapt and even SF specialists experience stress, leading to a higher trait integration. This suggests that while SF specialists are adapted to moderate waterlogging, extreme conditions may still overwhelm their adaptive mechanisms. We encourage future studies to explore the threshold of waterlogging and its impact on the physiology of trees in such environments.

Although drought is a significant threat to tropical forests, water excess, found in flooded soils or shallow water tables in the

Amazon basin, has been overlooked as being an important plant stressor in these particular habitats (Costa et al., 2023; Esteban et al., 2021; Parolin, 2001, 2010). In fact, during a typical year in central Amazonia, the main cause of tree mortality was due to rain (Aubry-Kientz et al., 2015; Fontes et al., 2018; Aleixo et al., 2019; Esquivel-Muelbert et al., 2020; O'Brien et al., 2024). Soil anoxic conditions that can occur in SF, cause a reduction in root conductance and increase stomatal closure, especially under high evaporative demand conditions (Kreuzwieser & Rennenberg, 2014). In dry conditions, trees with shallow root systems commonly found in SF habitats experience negative water balances because water availability in the upper soil layer is not sufficient to compensate for the increased tree water demands (Kunert et al., 2021). Root hydraulics are still missing from many studies, which could shed light on SF species strategies towards waterlogging. Root porosity, the proportion of longitudinally interconnected gas-filled spaces in root tissues enhancing gas diffusion, has been shown to provide an indication of the adaptability to environments with insufficient oxygen availability (Pan et al., 2022; Sojka, 1988).

4.3 | Generalist species change trait coordination along a topographic gradient

One of the most remarkable results to emerge from our study is a change in the level of trait coordination along the topographic gradient for generalist individuals (Figure 2a,b), illustrating a flexible trait syndrome. Generalist individuals appear to have a more constrained leaf trait syndrome on both extremes of the TWI gradient (Figure 2a,b). We expected generalist species to express a higher ITV (intraspecific trait variability), reflecting their phenotypic plasticity across the two contrasting studied habitats, as greater ITV could increase a species' fitness in more diverse environments (Bolnick et al., 2003). Nevertheless, we did not find that leaf ITV was higher for generalist species compared to specialist species (Figure 3). Low ITV for leaf traits are however in line with findings from other tropical forests (Fortunel et al., 2019; Schmitt & Boisseaux, 2023) or temperate forests (Dostál et al., 2017) that focused on morphological traits such as SLA, leaf dry matter content or plant height. The capacity to occupy a broader range of environments is therefore not reflected by a larger ITV for water-related traits or resource capture traits but by a change in trait coordination according to their topographic position. Low trait integration for generalists suggests weak constraints from the functional trade-offs among the traits measured, allowing various trait combinations. This flexibility permits a large number of generalist species to persist along the environmental gradient (He et al., 2021). However, we are aware of the sampling size limitation of our study, as most work on ITV has used a much bigger number of individuals per species. Nevertheless, recommendations for ideal robust samplings should be based on the same number of species and individuals per species in order to simultaneously

explore variation in leaf traits at the interspecific and intraspecific level (Schmitt & Boisseaux, 2023).

Being a generalist, growing in more diverse types of habitats, could also mean being able to cope with more diverse neighbours and the need to stay competitive. We here focused exclusively on the interaction between species and the abiotic environment, while we did not consider the effects of biotic interactions. Ecological niches are dynamic as the presence of one species constrains the presence of another species through interspecific competition (Gauze, 1934; Kermavnar et al., 2023; Kraft et al., 2015; Nemetschek et al., 2024). Considering other chemical traits such as leaf secondary metabolites could be used as a proxy for biotic interactions (Fine et al., 2004). Future research should include tree-to-tree interactions in order to assess how species respond to the abiotic environment while controlling for the presence and absence of other species in mediating this response.

5 | CONCLUSIONS

Our study provides an important advance to understanding the environmental filtering effect in Amazonian forests. The number of niche dimensions to explore species' strategies is potentially infinite. Here, functional species strategies were assessed along the soil water and nutrient dimension of a species' niche in the tropical forest of French Guiana. Our results suggested that species' identity and individual variation were the main drivers of single leaf functional trait variation and not the environment. However, we showed through multivariate analyses that the integration of both leaf chemical and water-related traits were more constrained with increasing waterlogging. Moderate drought events could alleviate this unique tree community to waterlogging stress water (Costa et al., 2023) but more intense and frequent droughts (Intergovernmental Panel on Climate Change (IPCC), 2023) could pile up stress on these already constrained trees. Moreover, the capacity to occupy a broader range of environments was not reflected by a larger ITV for generalist species but by the capacity to change the trait syndrome along a soil-moisture-nutrient gradient. Even though we focused on the leaf organ, as a critical component to understand variations in water and resource use among species, coordination of traits extend beyond leaves. Trait syndromes will likely also involve wood or root traits (Baraloto et al., 2010; Burton et al., 2020; Fortunel et al., 2014; Weemstra et al., 2023) which could extend our understanding of species habitat preferences to their mechanical support, resource allocation and below-ground strategies. Specifically, investigating the response to flooding through the trade-offs among root traits could offer great mechanistic insight to strategies employed by SF specialists for nutrient and water uptake (Cusack et al., 2021). Exploring the drivers of ecological strategies is critical to understand patterns of species' coexistence and biodiversity, especially in the framework of rapidly changing climates. These findings on trait-environment

interactions can ultimately be incorporated in joint species distribution models to determine potential shifts in species distribution.

AUTHOR CONTRIBUTIONS

Marion Boisseaux: investigation, methodology, validation, data curation, formal analysis, visualization, writing—original draft. Daniela Nemetschek: investigation, methodology, validation, data curation, writing—review and editing. Christopher Baraloto: conceptualization, resources, writing—review and editing. Benoit Burban: investigation. Angela Casado-Garcia: software. Jocelyn Cazal: investigation. Jeanne Clément: investigation, resources, writing—review and editing. Géraldine Derroire: conceptualization, methodology, supervision, writing—review and editing. Claire Fortunel: conceptualization, methodology, validation, data curation, writing—review and editing. Jean-Yves Goret: investigation. Jonathan Heras: software. Gaëlle Jaouen: conceptualization, validation, methodology, data management. Isabelle Maréchaux: methodology, writing—review and editing. Christine Scoffoni: investigation, resources, writing—review and editing. Ghislain Vieilledent: conceptualization, investigation, supervision, project administration, funding acquisition, writing—review and editing. Jason Vleminckx: resources, writing—review and editing. Sabrina Coste: conceptualization, investigation, supervision, writing—original draft. Heidy Schimann: conceptualization, supervision, writing—original draft. Clément Stahl: conceptualization, methodology, investigation, supervision, project administration, funding acquisition, writing—original draft. All authors gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

Functional trait data and scripts have been deposited on the Cirad DataVerse under the project name Metradica, at <https://doi.org/10.18167/DVN1/AYZDBY> (Boisseaux et al., 2024). The scripts supporting the results of this study can also be found on GitHub (https://github.com/mbthese/Metradica_FunctionalEcology).

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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. Discrimination of the habitats using the topographic wetness index (TWI).

Figure S2. The 21 selected species' phylogeny.

Figure S3. Indval values for the studied species.

Figure S4. Variation of leaf trait values among species.

Figure S5. Scatter plots showing the relationship between DBH and leaf traits for 21 species.

Figure S6. The Dawkins index classes of crown position.

Figure S7. Trait variation according to the Dawkins index classes of crown position.

Figure S8. Principal components analysis (PCA) among eight leaf traits for 552 trees belonging to 21 studied species ($n = 552$).

Figure S9. Trait contributions to first four principal component axes among leaf traits.

Figure S10. Principal components analysis with the third axis.

Figure S11. Spearman correlation coefficients among leaf traits for each category of species preference.

Table S1. Sampling sites supplementary information.

Table S2. Individuals per species collected in the three forest sites.

Table S3. Species chosen for the study according to the indicator values (Indval) within each habitat in French Guiana.

Table S4. Permutational manova analysis and post-hoc pairwise analysis.

Table S5. Pairwise tables for the spearman correlation.

Table S6. Model summary for each trait from linear mixed effect model (Equation 1).

Table S7. Tree height and tree DBH ranges.

Appendix S1. Network analysis.

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