

# Disentangling the effects of environment and ontogeny on tree functional dimensions for congeneric species in tropical forests

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## Summary

- Soil water and nutrient availability are key drivers of tree species distribution and forest ecosystem functioning, with strong species differences in water and nutrient use. Despite growing evidence for intraspecific trait differences, it remains unclear under which circumstances the effects of environmental gradients trump those of ontogeny and taxonomy on important functional dimensions related to resource use, particularly in tropical forests.
- Here, we explore how physiological, chemical, and morphological traits related to resource use vary between life stages in four species within the genus *Micropholis* that is widespread in lowland Amazonia. Specifically, we evaluate how environment, developmental stage, and taxonomy contribute to single-trait variation and multidimensional functional strategies.
- We find that environment, developmental stage, and taxonomy differentially contribute to functional dimensions. Habitats and seasons shape physiological and chemical traits related to water and nutrient use, whereas developmental stage and taxonomic identity impact morphological traits—especially those related to the leaf economics spectrum.
- Our findings suggest that combining environment, ontogeny, and taxonomy allows for a better understanding of important functional dimensions in tropical trees and highlights the need for integrating tree physiological and chemical traits with classically used morphological traits to improve predictions of tropical forests' responses to environmental change.

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## Introduction

Recent modelling advances have incorporated tree physiological responses to soil nutrients and water availability to evaluate the impact of predicted changes in nitrogen (N) deposition and rainfall regimes on forest ecosystems (Dybzinski *et al.*, 2015; Fariior *et al.*, 2015). The majority of these models uses a 'mean field' approach where all individual trees within a species exhibit the same response to environmental conditions. However, there is growing evidence that conspecific individuals can differ markedly in their response to soil nutrients and water availability (Paine *et al.*, 2011; Derroire *et al.*, 2018). Understanding the sources of intraspecific variation in tree species responses to the environment is crucial to improve our ability to make accurate predictions of forest responses to global change.

Tropical forests represent key ecosystems because they contribute considerably both to world-wide biodiversity and to the carbon (C) cycle (Gaston, 2000; Malhi *et al.*, 2002). Nevertheless, their C uptake is strongly limited by the reduced photosynthesis and increased tree mortality that accompany the increasing frequency and intensity of droughts under climate change (Brienen *et al.*, 2015; Frank *et al.*, 2015). Tropical tree distribution is strongly shaped by spatiotemporal variation in water availability

(Engelbrecht *et al.*, 2007; Bartlett *et al.*, 2016; Esquivel-Muelbert *et al.*, 2017), but we are still lacking detailed information on the physiological response to drought for the vast majority of tropical tree species because of time and resource constraints (Anderegg *et al.*, 2018). A pressing challenge for ecologists is to evaluate the potential for relatively easy-to-measure traits to capture essential features of tropical tree physiology (O'Brien *et al.*, 2017; Santiago *et al.*, 2018; Maréchaux *et al.*, 2018; Barros *et al.*, 2019).

Recent trait-based studies have leveraged interspecific trait differences to understand how climate and soil gradients shape species distributions in tropical systems (Bartlett *et al.*, 2016; Uriarte *et al.*, 2018; Oliveira *et al.*, 2019). In particular, drier climate and poorer soils have been found to favor species with tougher leaves and denser wood that grow more slowly but have higher survival rates, notably during drought spells (Poorter *et al.*, 2008; Fortunel *et al.*, 2014; Uriarte *et al.*, 2016). However, most studies so far have used species mean trait values; despite some intensive sampling efforts (e.g. Baraloto *et al.*, 2010), though, the importance of intraspecific trait variability for most tropical tree species remains largely unknown.

Trees are long-lived organisms that increase in size and structural complexity during their ontogenetic development. Leaf physiological, morphological, and chemical traits change because

of variation in light availability and evaporative demand with tree height (Russo & Kitajima, 2016). In addition, wood traits vary because of mechanical and hydraulic constraints arising with increased transport distance between roots and leaves (Hietz *et al.*, 2017). Tree performance in terms of growth and mortality can subsequently be optimized by different leaf and wood trait values between developmental stages (Hérault *et al.*, 2011; Lasky *et al.*, 2015). Yet, few studies have explored how leaf and wood trait variations during tree development contribute to tropical tree species distribution and functioning across environmental gradients.

Here, we investigate changes in physiological, morphological, and chemical traits of tropical trees between ontogenetic stages across forest habitats and seasons in French Guiana. We measured traits in leaves and wood of seedlings, saplings, and adults from four species within the common genus *Micropholis* (Sapotaceae), allowing for a control of species evolutionary history. These species exhibit contrasting distributions across the three main forest habitats of lowland South American rainforests (clay terra firme forests, seasonally flooded forests, and white sand forests) that differ in soil nutrients and water availability (Baraloto *et al.*, 2011). To capture seasonal differences in soil water availability in French Guiana (Bonal *et al.*, 2008), we replicated our sampling in the wet and dry seasons. We specifically asked the following two questions:

Q1. What is the relative contribution of habitat, season, developmental stage, and taxonomic identity to trait variation?

We expect habitat and developmental stage to be the main contributors to variation in morphological and chemical traits via changes in soil nutrients and light levels, whereas we expect seasonal changes to drive variation in physiological traits via differences in soil water availability (Griffin-Nolan *et al.*, 2018). Because our experimental design constrains the phylogenetic depth among our species, we expect species contribution to trait variation to be comparable across traits.

**Table 1** Environmental factors in the three focal forest habitats.

Group	Variable	Unit	Seasonally flooded	Terra firme	White sand
Climate	Mean annual rainfall	mm yr <sup>-1</sup>	2471	2471	2471
	Dry-season index	days	36.8	36.8	36.8
Soil	Sand	%	95	75	98
	Silt	%	2	2	0
	Clay	%	3	23	2
	N	%	0.099	0.083	0.023
	C	%	2.2	1.26	0.51
	Olsen phosphorus	ppm	1.3	2.8	<0.5
	K	mEq/100 g	0.05	0.07	0.01
	Water availability (wet season)	%	42.6	24.1	7.9
Stand	Water availability (dry season)	%	37.4	10.7	3.1
	Number of species		104	114	78
	Stem density (> 2.5 cm DBH)	ha <sup>-1</sup>	2370	1974	4552
	Basal area (> 2.5 cm DBH)	m <sup>2</sup> ha <sup>-1</sup>	52.19	34.64	30.31
	Aboveground biomass (> 2.5 cm DBH)	Mg ha <sup>-1</sup>	493.29	351.76	262.33

Dry-season index was calculated as the maximum number of consecutive days receiving < 10 mm of precipitation in a given calendar year, averaged over the 11 yr for which data were available from all sites. Details on soil measurements and stand calculations are available in Baraloto *et al.* (2011). DBH, diameter at breast height.

Q2. How do habitat, season, developmental stage, and taxonomic identity impact functional strategies?

Combining morphological, chemical, and physiological traits to define functional strategies of tropical trees, we expect that the effects of habitat, season, and developmental stage would be detectable along different functional axes, in line with their relative contribution to individual trait variation.

## Material and Methods

### Study site

We sampled broad environmental gradients representative of lowland South American rainforests, drawing from a network of 36 modified 0.5 ha Gentry plots in French Guiana that cover the more commonly studied clay terra firme forests in addition to seasonally flooded forests and white sand forests (Baraloto *et al.*, 2011). These habitats represent broad gradients of soil nutrients availability, drought, and flooding (Table 1). For this study, we selected one plot per habitat in Laussat, in the western region of French Guiana. We measured surface soil water availability in the focal three plots using a portable moisture sensor (Trime Pico64; IMKO Micromodultechnik GmbH, Ettlingen, Germany) and found decreasing soil humidity from seasonally flooded forest to terra firme forest to white sand forest, further accentuated during the dry season (Table 1).

### Tree species

We focused on the genus *Micropholis* (Sapotaceae), which is widespread in Amazonia (ter Steege *et al.*, 2013). Because it is logistically challenging to measure tree physiology in remote tropical sites, we focused on four focal species that together represent a quarter of the genus in French Guiana: *Micropholis egensis*, *Micropholis guyanensis*, *Micropholis venulosa*, and *Micropholis*

*melinoniana*. At the nearby Paracou research station in French Guiana, where all stems above 10 cm DBH (diameter at breast height) have been monitored yearly since 1984 (Gourlet-Fleury *et al.*, 2004), these species vary in maximum sizes (49.50 cm, 41.74 cm, 42.29 cm and 50.80 cm DBH, respectively) and annualized diameter growth rates (1.76 mm yr<sup>-1</sup>, 2.03 mm yr<sup>-1</sup>, 1.08 mm yr<sup>-1</sup>, and 1.93 mm yr<sup>-1</sup>, respectively, over the period 1984–2018). The focal species exhibit contrasting abundances between the three forest habitats (Table 2): *M. egensis* is most abundant in terra firme forests, *M. guyanensis* in seasonally flooded forests, and *M. venulosa* in white sand forests, whereas *M. melinoniana* has similar abundances across all three habitats.

In July 2012, we mapped all individuals of the four focal species in the three study plots and recorded their height and diameter (at the root collar for seedlings and at breast height for saplings and adult trees). We sampled individuals at three distinct stages of development (seedling, sapling, adult) based on tree size and architecture (Table 2). Seedlings are juvenile individuals with height ≤ 80 cm, generally unbranched or with a few rare epicormic branches resulting from traumas. Saplings are juvenile individuals with height > 80 cm and DBH < 5 cm. Their architecture is organized around a main orthotropic axis bearing sequential plagiotropic branches. Saplings can carry up to three branching orders and sometimes carry epicormic twigs reflecting responses to traumas or low light resources (Nicolini *et al.*, 2003). Finally, subadult and adult trees are individuals with height > 6 m and DBH > 5 cm whose crowns are formed by numerous reiterated complexes (Nicolini & Chanson, 2000; Barthélémy & Caraglio, 2007).

### Trait measurements

At the end of the wet and dry seasons in 2012, we sampled all selected individuals for each of the four focal species in each of

the three forest habitats and measured physiological, chemical, and morphological traits that capture key functions (Table 3). To standardize light levels between stages, we conducted leaf measurements on mature leaves from the last fully expanded growth unit found in the understory. To determine leaf gas exchange, we selected the last fully expanded leaf on (1) a lateral branch for sapling and adult individuals and (2) the main stem for seedling individuals. Detached branches (≥ 2 m long) were immediately recut under water to restore hydraulic connectivity without affecting leaf dark respiration and photosynthesis (Turnbull *et al.*, 2003; Cavaleri *et al.*, 2008; Rowland *et al.*, 2015). All gas exchange measurements were made using a portable infrared gas analyzer (CIRAS-1; PP Systems, Hitchin, UK), setting the leaf chamber block temperature to 28°C (close to ambient temperature) and the air flow through the chamber at 400 μmol s<sup>-1</sup>. Leaves were exposed at saturating irradiance (2000 μmol m<sup>-2</sup> s<sup>-1</sup>) for 10 min in the chamber before measuring light-saturated photosynthesis *A*<sub>sat</sub> and stomatal conductance *g*<sub>sat</sub> at ambient atmospheric CO<sub>2</sub> (400 ppm). We also measured photosynthesis at 1000 μmol m<sup>-2</sup> s<sup>-1</sup> (*A*<sub>1000</sub>) but discarded it from subsequent analyses because it was strongly correlated with *A*<sub>sat</sub> (*r*<sub>Pearson</sub> = 0.97, *P* < 0.001). Leaves were then darkened for 30 min to ensure steady-state conditions before measuring dark respiration rate *R*<sub>dark</sub>. To examine leaf water status, we sampled the second-to-last fully expanded leaf to determine leaf hydraulic potential at predawn ( $\Psi_{pd}$ , between 05:30 h and 07:00 h) and at midday ( $\Psi_{md}$ , between 11:30 h and 13:00 h) using a Scholander-type pressure chamber (model 1000; PMS Instruments, Corvallis, OR, USA). For leaf morphological and chemical traits, we sampled three fully expanded leaves per individual. We estimated leaf chlorophyll content (LChl) by averaging three measurements from a Minolta SPAD 502DL meter (Spectrum Technologies, Aurora, IL, USA) using calibrations from Coste *et al.* (2010). We measured leaf thickness (L<sub>thick</sub>) as the mean of three

**Table 2** Height, diameter, relative abundance, and sample size between the three forest habitats of the four focal *Micropholis* species.

Species	Stage	Height (cm)	Diameter (mm)	Seasonally flooded	Terra firme	White sand
<i>Micropholis egensis</i>	Abundance (%)			0.08	0.20	0.15
	Seedling	29.55	3.44	10	6	10
	Sapling	200.62	10.31	8	6	6
	Adult	960.00	70.27	6	0	4
<i>Micropholis guyanensis</i>	Abundance (%)			0.60	0.51	0.25
	Seedling	42.44	5.00	8	6	4
	Sapling	234.65	11.46	6	8	6
	Adult	1335.71	146.73	4	6	4
<i>Micropholis melinoniana</i>	Abundance (%)			0.03	0.02	0.02
	Seedling	39.40	4.76	0	2	0
	Sapling	558.00	41.74	2	6	2
	Adult	1721.25	227.16	4	6	6
<i>Micropholis venulosa</i>	Abundance (%)			0.03	0.17	0.22
	Seedling	23.42	1.97	0	4	6
	Sapling	246.50	12.66	8	6	6
	Adult	1530.00	129.93	4	0	6

Height and diameter values are the average across sampled individuals for each developmental stage. Diameter values correspond to the diameter at the base of the root collar for seedlings and the diameter at breast height (DBH; 1.30 m) for saplings and adult trees. Relative abundance data correspond to occurrence of trees > 2.5 cm DBH in 36 modified 0.5 ha Gentry plots across the three habitats as part of previous work (Baraloto *et al.*, 2011).

**Table 3** Leaf and wood functional traits.

Trait	Abbreviation	Unit	Organ	Type	Mechanisms
Light-saturated photosynthesis	$A_{\text{sat}}$	$\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$	Leaf	Physiological	Resource capture
Light-saturated stomatal conductance	$g_{\text{sat}}$	$\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$	Leaf	Physiological	Water loss
Dark respiration rate	$R_{\text{dark}}$	$\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$	Leaf	Physiological	Resource capture, maintenance
Midday leaf water potential	$\Psi_{\text{md}}$	MPa	Leaf	Physiological	Drought resistance, water status
Predawn leaf water potential	$\Psi_{\text{pd}}$	MPa	Leaf	Physiological	Soil water potential
Leaf chlorophyll content	LChl	$\mu\text{g mm}^{-2}$	Leaf	Chemical	Resource capture
Foliar carbon	LCC	$\text{cg g}^{-1}$	Leaf	Chemical	Resource capture and defense
Foliar nitrogen	LNC	$\text{cg g}^{-1}$	Leaf	Chemical	Resource capture and defense
Foliar phosphorus	LPC	$\mu\text{g g}^{-1}$	Leaf	Chemical	Resource capture
Foliar potassium	LKC	$\mu\text{g g}^{-1}$	Leaf	Chemical	Resource capture
Foliar $^{13}\text{C}$ composition	$L^{13}\text{C}$	‰	Leaf	Chemical	Drought resistance
Leaf area	LA	$\text{cm}^2$	Leaf	Morphological	Resource capture
Specific leaf area	SLA	$\text{m}^2 \text{ kg}^{-1}$	Leaf	Morphological	Resource capture and defense
Leaf tissue density	LTD	$\text{g cm}^{-3}$	Leaf	Morphological	Resource capture and defense
Leaf thickness	Lthick	mm	Leaf	Morphological	Resource capture and defense
Leaf toughness	Ltough	N	Leaf	Morphological	Resource capture and defense
Wood specific gravity	WSG	no unit	Wood	Morphological	Transport, structure, and defense

measurements with a digital micrometer (Mitutoyo Instruments, Singapore). We determined leaf toughness (Ltough) as the average of three punch tests with a Chatillon penetrometer (Ametek, Largo, FL, USA). We evaluated scanned leaf area (LA) by image analyses with WINFOLIA software (Regent Instruments, Toronto, ON, Canada). Leaves were dried at 60°C for 72 h and their dry mass was weighed to determine specific leaf area (SLA, LA divided by its dry mass) and leaf tissue density (dry mass divided by the product between LA and Lthick). We then ground leaves together to fine powder using a ball mill (Retsch MM200; Retsch GmbH & Co., Haan, Germany). Their C and N concentrations and  $^{13}\text{C}$  isotopic ratios were determined using an elemental analyzer and mass spectrometer at the University of California, Davis. Foliar C isotope composition ( $L^{13}\text{C}$ , ‰) followed Farquhar, Ehleringer & Hubick (1989), using the conventional Pee Dee Belemnite standard. Leaf phosphorus (P) and potassium (K) analyses were conducted by the Soil and Plant Agricultural Laboratory at the Louisiana State University using an inductively coupled spectrometer on nitric acid–hydrogen peroxide digests of 500 mg of plant tissue. To determine wood specific gravity (WSG), we harvested wood samples on a lateral branch for sapling and adult individuals and on the main stem for seedling individuals (only at the end of the experiment). We removed outer bark, phloem, and pith wider than 1 mm in diameter. We estimated stem saturated volume on the principle of water displacement using a Sartorius density determination kit (Goettingen, Germany). Stem samples were then dried at 103°C for 72 h to determine their dry mass. Stem specific gravity was calculated as the dry mass divided by the saturated volume (Williamson & Wiemann, 2010).

### Data analysis

We used variance partitioning to evaluate the relative contribution of habitat, season, developmental stage, and species identity on each trait separately. We then used redundancy analysis to

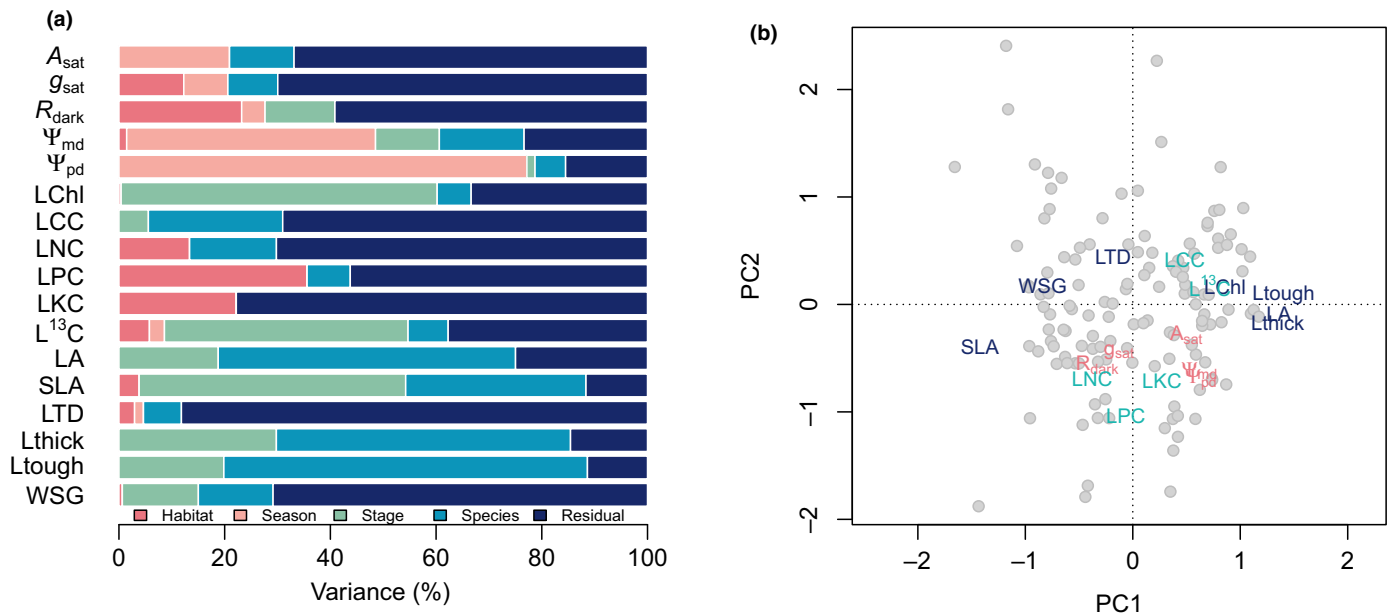
explore similarities in how physiological, morphological, and chemical traits respond to habitat, season, developmental stage, and species identity. In addition, we used generalized linear models to test the effects of habitat, season, developmental stage, and species identity on each trait separately. We used the Spearman correlation test to determine pairwise relationships between traits. We performed a principal component analyses (PCA) to illustrate the relationships and used a MANOVA to test for multivariate differences between habitat, season, developmental stage, and species identity. Finally, we used Mantel tests to evaluate whether matrices of pairwise correlations between all traits were similar among forest habitats, dry and wet seasons, developmental stages, and the four focal *Micropholis* species. All traits were log-transformed before analysis. All analyses were conducted in the R v.3.6.1 statistical platform (R Development Core Team, 2019) using packages MOMOCS (Bonhomme *et al.*, 2014) and VEGAN (Dixon, 2003).

## Results

### Contribution of habitat, season, developmental stage, and taxonomic identity to single-trait variation

Habitat, season, developmental stage, and species identity varied in their relative contributions between trait types (Fig. 1a). As predicted, habitat mostly contributed to chemical traits (foliar N (LNC), foliar P (LPC), and foliar K (LKC)), but was also the main contributor to  $g_{\text{sat}}$  and  $R_{\text{dark}}$ . In line with our prediction, season contributed to physiological traits, and especially strongly to  $A_{\text{sat}}$ ,  $\Psi_{\text{md}}$ , and  $\Psi_{\text{pd}}$ . As expected, developmental stage was the main driver of LChl and  $L^{13}\text{C}$ , and strongly contributed to most morphological traits (LA, SLA, Lthick, Ltough, and WSG). Species identity mainly drove variation in LA, Lthick, and Ltough, and strongly contributed to foliar C (LCC), LNC, SLA, and WSG. Looking at how the 17 traits studied responded to habitat, season, developmental stage, and species identity





**Fig. 1** (a) Variance partitioning of trait values across habitat, season, developmental stage, and species identity. (b) Redundancy analysis of trait response to habitat, season, developmental stage, and species identity.  $A_{\text{sat}}$ , light-saturated photosynthesis;  $g_{\text{sat}}$ , light-saturated stomatal conductance;  $R_{\text{dark}}$ , dark respiration rate;  $\Psi_{\text{md}}$ , midday leaf water potential;  $\Psi_{\text{pd}}$ , predawn leaf water potential; LChl, leaf chlorophyll content; LCC, foliar carbon; LNC, foliar nitrogen; LPC, foliar phosphorus; LKC, foliar potassium;  $L^{13}\text{C}$ , foliar  $^{13}\text{C}$  composition; LA, leaf area; SLA, specific leaf area; LTD, leaf tissue density; Lthick, leaf thickness; Ltough, leaf toughness; WSG; wood specific gravity.

(Fig. 1b), we found that morphological traits mostly aligned with the first axis of the redundancy analysis that related to developmental stage and species identity, whereas physiological and chemical traits generally overall followed the second axis that was dominated by habitat and season.

Traits strongly varied between the three studied forest habitats (Table 4). In particular,  $A_{\text{sat}}$ ,  $g_{\text{sat}}$ , and  $R_{\text{dark}}$  were higher in terra firme forest than in seasonally flooded and white sand forests.  $\Psi_{\text{md}}$  was less negative in seasonally flooded forest than in terra firme forest and white sand forest. These variations in physiological traits were mirrored by changes in morphological and chemical traits. In particular, SLA, Lthick, and Ltough were higher in seasonally flooded forest than in terra firme and white sand forests. LNC showed a somewhat similar behavior, with higher LNC in seasonally flooded and terra firme forests than in white sand forest. However, LChl increased from seasonally flooded forest to terra firme forest to white sand forest.  $L^{13}\text{C}$  increased from seasonally flooded forest to terra firme forest to white sand forest.

Physiological traits varied significantly between seasons (Table 4):  $A_{\text{sat}}$  was higher in the wet season than in the dry season, and  $\Psi_{\text{md}}$  was less negative during the wet season than during the dry season. As predicted, morphological and chemical traits did not vary between seasons.

Most traits varied significantly with developmental stage (Supporting Information Fig. S1; Table 4).  $A_{\text{sat}}$  increased,  $R_{\text{dark}}$  decreased, and  $\Psi_{\text{md}}$  was less negative from seedlings to saplings to adult trees. In addition, SLA decreased with developmental stage, whereas LChl, Lthick, and Ltough showed the opposite pattern. Contrary to our expectation, adult trees had less dense wood than seedlings and saplings, and LNC was similar between

developmental stages. As predicted, trait variations between developmental stages were overall consistent between habitats (Fig. S2). In particular, variation in  $A_{\text{sat}}$ ,  $R_{\text{dark}}$  rate, and  $\Psi_{\text{md}}$  with developmental stage were consistent between habitats. Similarly, LA and Ltough increases from seedlings to saplings to adult trees were consistent between habitats. Conversely, though LNC, LPC, and LKC did not vary with developmental stage when pooling all data together, they showed significant differences between developmental stages within habitats. For instance, these chemical traits increased with developmental stage in white sand forests but showed the opposite pattern in terra firme forests, with overall little to no variation in seasonally flooded forests. In line with our prediction, trait differences between developmental stages were similar between dry and wet seasons (Fig. S3). Noticeably, variation in  $\Psi_{\text{md}}$  with developmental stage was steeper during the dry season than the wet season. Conversely, the increase in  $L^{13}\text{C}$  with increasing developmental stage was comparable during the dry season than the wet season.

The four congeneric species varied strongly with respect to their traits (Table 4). *Micropholis guyanensis* exhibited higher  $A_{\text{sat}}$ , lower SLA and LNC, and tougher leaves than the other three species. At the opposite of the trait spectrum, *M. venulosa* exhibited lower  $A_{\text{sat}}$ , associated with higher SLA, LNC, and WSG and lower Lthick and Ltough than the other species.

#### Effects of habitat, season, developmental stage, and taxonomic identity on multi-trait variation

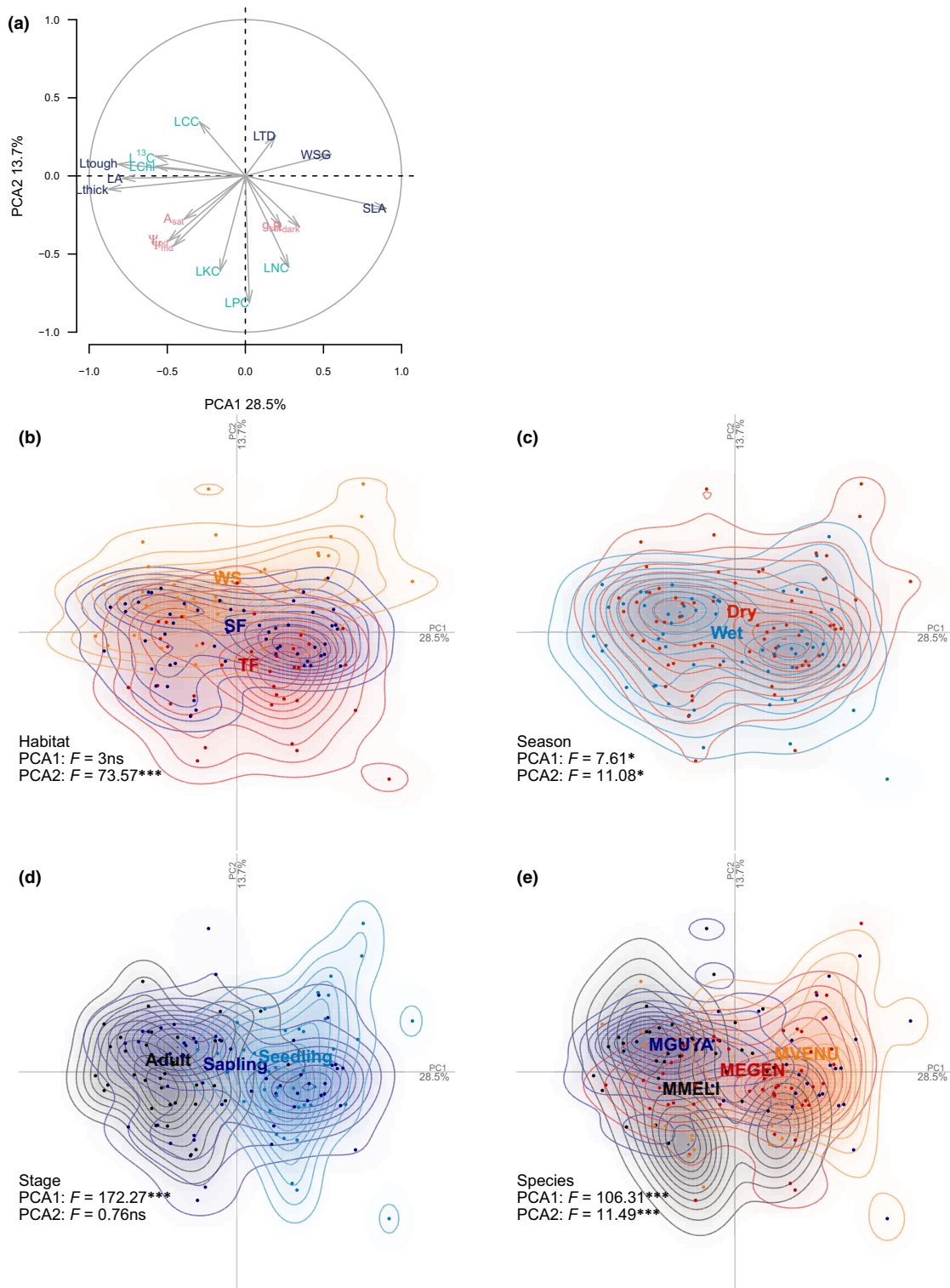
We found a limited number of significant pairwise correlations between physiological, morphological, and chemical traits (Table S1).  $A_{\text{sat}}$  increased with increasing LA and Ltough.  $R_{\text{dark}}$

**Table 4** Generalized linear model effects of habitat, season, developmental stage and species identity on log-transformed traits.

Trait	Habitat			Season			Stage			Species						
	F	SF	TF	WS	F	Dry	Wet	F	Seedling	Sapling	Adult	F	Seedling	Sapling	Adult	
$A_{\text{sat}}$	10.50***	b	a	b	22.91***	b	a	4.13*	a	a	a	5.77***	b	a	a	5.77***
$g_{\text{sat}}$	8.51***	b	a	b	0.00 ns	a	a	5.58**	b	a	a	0.12 ns	a	a	a	0.12 ns
$R_{\text{dark}}$	14.90***	b	a	b	0.23 ns	a	a	20.65***	c	b	a	1.45 ns	a	a	a	1.45 ns
$\Psi_{\text{mid}}$	38.48***	a	b	c	70.38***	b	a	36.18***	a	b	b	7.56***	a	ab	a	7.56***
$\Psi_{\text{pd}}$	104.79***	a	b	c	220.17***	b	a	47.14***	a	b	b	6.28**	ab	a	a	6.28**
LChI	3.84*	b	ab	a	2.91 ns	a	a	98.98***	a	b	b	9.24***	b	a	a	9.24***
LCC	0.44 ns	a	a	a	0.35 ns	a	a	6.75**	a	b	b	22.15***	c	a	b	22.15***
LNC	12.10***	a	a	b	0.20 ns	a	a	0.46 ns	a	a	a	13.50***	bc	c	ab	13.50***
LPC	39.39***	b	a	c	0.00 ns	a	a	2.74 ns	a	a	a	7.96***	a	b	a	7.96***
LKC	18.62***	b	a	c	0.13 ns	a	a	0.54 ns	a	a	a	6.14***	a	ab	a	6.14***
$L^{13}\text{C}$	14.26***	c	b	a	0.49 ns	a	a	71.77***	a	b	c	3.08*	ab	b	a	3.08*
LA	14.03***	b	a	b	0.01 ns	a	a	46.45***	a	a	a	117.29***	b	a	b	117.29***
SLA	19.01***	a	b	b	1.41 ns	a	a	194.48***	c	b	b	115.06***	b	d	c	115.06***
LTD	4.44*	ab	b	a	1.29 ns	a	a	0.19 ns	a	a	a	8.69***	c	ab	bc	8.69***
Lthick	19.71***	b	a	b	0.47 ns	a	a	110.61***	a	b	b	150.23***	a	a	a	150.23***
Ltough	15.01***	b	a	b	0.04 ns	a	a	72.17***	a	b	b	210.44***	b	a	b	210.44***
WSG	1.83 ns	a	a	a	0.00 ns	a	a	13.61***	b	a	a	12.43***	b	b	b	12.43***

F statistics are shown with significance test (\*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ; \*\*\*,  $P < 0.001$ ; ns, nonsignificant). Post-hoc Tukey's honestly significant difference test for habitat, season, stage, and species identity are indicated with lowercase letters.  $A_{\text{sat}}$ , light-saturated photosynthesis;  $g_{\text{sat}}$ , light-saturated stomatal conductance;  $R_{\text{dark}}$ , dark respiration rate;  $\Psi_{\text{mid}}$ , midday leaf water potential;  $\Psi_{\text{pd}}$ , predawn leaf water potential; LChI, leaf chlorophyll content; LCC, foliar carbon; LNC, foliar nitrogen; LPC, foliar phosphorus; LKC, foliar potassium;  $L^{13}\text{C}$ , foliar  $^{13}\text{C}$  composition; LA, leaf area; SLA, specific leaf area; LTD, leaf tissue density; Lthick, leaf thickness; Ltough, leaf toughness; WSG, wood specific gravity.

SF, seasonally flooded forest; TF, terra firme forest; WS, white sand forest.



**Fig. 2** Principal components analysis (PCA) on 17 traits from four *Micropholis* species. (a) Correlation circle of trait data, where physiological traits are shown in salmon, chemical traits in turquoise, and morphological traits in blue.  $A_{sat}$ , light-saturated photosynthesis;  $g_{sat}$ , light-saturated stomatal conductance;  $R_{dark}$ , dark respiration rate;  $\Psi_{md}$ , midday leaf water potential; LChl, leaf chlorophyll content; LCC, foliar carbon; LNC, foliar nitrogen; LPO, foliar phosphorus; LKCO, foliar potassium; L<sup>13</sup>C, foliar <sup>13</sup>C composition; LA, leaf area; SEA, specific leaf area; LTD, leaf tissue density; Lthick, leaf thickness; Lough, leaf toughness; WSG, wood specific gravity. (b) Habitat clusters, where terra firme (TF) forests are shown in red, seasonally flooded (SF) forest in blue, and white sand (WS) forests in yellow. (c) Season clusters, where wet season is shown in blue and wet season in orange. (d) Stage clusters, where adults are shown in gray, saplings in blue, and seedlings in turquoise. (e) Species clusters, where *Micropholis egensis* (MEGEN) is shown in red, *Micropholis guyanensis* (MGUYA) in blue, *Micropholis venulosa* (MVENU) in yellow, and *Micropholis melinoniana* (MMELI) in gray. Variances explained by the first two PCA axes (PCA1 and PCA2) are shown. In panels (b)–(e), MANOVA tests and significance indicate cluster differences along PCA1 and PCA2. \*,  $P < 0.05$ ; \*\*\*,  $P < 0.001$ ; ns, nonsignificant.

increased with increasing SLA and decreasing  $L^{13}C$ .  $\Psi_{md}$  increased with increasing LChl and Lthick. Together, physiological, morphological and chemical traits defined two main axes of trait variation (Fig. 2a): a first axis corresponding to the leaf economics spectrum (sensu Wright *et al.*, 2004) and a second axis corresponding to water and nutrient use. Habitats strongly segregated along the second PCA axis (Fig. 2b), whereas developmental stages significantly separated along the first PCA axis (Fig. 2d). Seasons and species differed along the two PCA axes (Fig. 2c,e). In addition, matrices of pairwise correlations between all 17 traits were significantly similar between forest habitats, dry and wet seasons, developmental stages, and the four focal *Micropholis* species (Table S2).

## Discussion

An important challenge to strengthen predictions for how tropical forests will respond to climate change is to improve our understanding of how multiple factors shape tropical tree response to water and nutrient availability (Condit *et al.*, 2013; Fortunel *et al.*, 2016; Uriarte *et al.*, 2018; Schwartz *et al.*, 2019). Functional traits allow examining species distributions across broad environmental gradients only in that we assume traits to be tightly linked to the underlying key physiological processes driving species response to the environment (Violle *et al.*, 2007). Despite growing evidence of the importance of intraspecific variability for trait variation in the landscape (Benito Garzón *et al.*, 2011; Lasky *et al.*, 2015; Siefert *et al.*, 2015; Spasojevic *et al.*, 2016), its extent remains largely unknown in tropical tree species (Bastias *et al.*, 2017; Fortunel *et al.*, 2019). Investigating variation in physiological, morphological, and chemical traits between developmental stages in four tropical tree species across forest habitats and between seasons, we provide an important test to disentangle the effects of environment, ontogeny, and taxonomic identity on functional dimensions in tropical trees.

We find that the relative contribution of habitat, season, developmental stage, and taxonomic identity varies between trait types. As predicted, variation in morphological and chemical traits is mainly driven by habitat and developmental stage. In line with previous work in tropical forests, forest habitat appears as an important driver of leaf chemical traits (Kraft *et al.*, 2008; Katabuchi *et al.*, 2012; Fortunel *et al.*, 2014), whereas developmental stage mostly impacts morphological traits (Kitajima *et al.*, 2013; Cobo-Quinche *et al.*, 2019). Interestingly, variation in physiological, morphological, and chemical traits with developmental stage is overall independent of habitats, which suggests that ontogenetic trajectories are primarily shaped by inherent developmental constraints within species. In particular, although there is some degree of plasticity during leaf expansion, leaf morphology and chemistry are mostly fixed once the leaf is fully expanded. Therefore, morphological and chemical traits are often too integrative to be tightly linked to physiological variations that occur at daily or seasonal scales (Paine *et al.*, 2015; Yang *et al.*, 2018).

In line with our prediction, variation in physiological traits is primarily driven by season, and to a lesser extent by habitat, developmental stage, and species identity. Previous work conducted on saplings of *M. egensis* and *M. guyanensis* at our study site showed

variation in leaf phenology between species (with rhythmic and continuous leaf production, respectively) that could further contribute to these physiological differences (Lamarre *et al.*, 2012). Our work suggests that using a ‘mean field’ approach (here, using mean trait values to represent species physiology) would fail to capture important seasonal patterns in species functioning. This further emphasizes the need to incorporate seasonally measured physiological traits along with leaf phenology information in experiments and models to gain a more mechanistic understanding of how tropical tree species will respond to spatiotemporal variation in water availability (Bartlett *et al.*, 2016; Anderegg *et al.*, 2016; Weng *et al.*, 2017; Maréchaux *et al.*, 2018).

Overall, we show that bigger trees exhibit lower SLA and sapwood density, but greater leaf chlorophyll content, thickness, and toughness. They also have greater light-saturated photosynthesis, lower dark respiration, and less negative midday leaf water potential. These results together suggest that earlier developmental stages tend to build cheap leaves with a fast turnover that are efficient at capturing light in the shaded understory, but invest in sturdy stems to minimize cavitation risk (Markesteijn & Poorter, 2009) and avoid damage by herbivores and pathogens (Kitajima & Poorter, 2008). As trees grow and experience increasing light levels, they may invest less in wood density in branches but more in heartwood in the main stem (Lehnebach *et al.*, 2019), and start building thicker and tougher leaves that can layer more palisade mesophyll cells to improve light interception (Osnas *et al.*, 2018).

Contrary to our expectation, we find that taxonomic identity varies strongly in its contribution to trait variation: it was a strong contributor to most morphological traits, with a lesser effect on physiological and chemical traits. Despite our experimental design that purposefully limited phenotypic range by focusing on species within a single genus, species show strong trait differentiation along the two main functional dimensions, suggesting that they occupy distinct niche space both in terms of leaf physiology and leaf economics. As the four focal *Micropholis* species have contrasting habitat preferences, such strong trait differences between species may play a role in local biotic interactions and shape species distributions across environmental gradients (Fortunel *et al.*, 2018; Schwartz *et al.*, 2019).

To somewhat balance our limited sampling size due to logistics constraints, we focused on a genus that is widespread across lowland Amazonia and that contains species with contrasting distributions in the three main forest habitats found in the Amazon region. This is a first step into evaluating how environmental variation and developmental stage influence ecological strategies in tropical tree species. We may be able to generalize our findings to similarly widely distributed genera with habitat specialist species, such as *Protium* or *Inga* (ter Steege *et al.*, 2013). However, future work will need to improve the phylogenetic coverage to assess the extent to which we can generalize the role of environment and developmental stage in shaping species functional strategies.

## Conclusion

Examining how environment, developmental stage, and taxonomic identity contribute to important physiological, chemical,



and morphological traits in tropical tree species in lowland Amazonia, we show that habitat and season strongly shape leaf physiology and chemistry, which highlights their importance in driving water and nutrient use in tropical trees. In addition, we find that developmental stages and species identity are the main drivers of leaf morphology, which suggests that some distinct aspects of ecological niches between species are conserved as trees grow into adults. Our study provides an important first step in better understanding the drivers of ecological strategies in tropical trees and suggests ways forward to improve predictions of the future of tropical forests with changes in water and nutrient availability.

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## Author contributions

CF designed the study, formatted data, performed the analyses, and wrote the first draft of the manuscript. CF and CB installed the plot network and collected floristics data. CF, CB, CS, PH and EN collected data, contributed to revisions of the manuscript, and gave final approval for publication.

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## Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

**Fig. S1** Effect of developmental stages on traits.

**Fig. S2** Effect of the interaction between developmental stages and habitat types on traits.

**Fig. S3** Effect of the interaction between developmental stages and seasons on traits.

**Table S1** Pairwise correlations among log-transformed traits.

**Table S2** Mantel tests between matrices of pairwise correlations between all physiological, morphological and chemical traits by habitat, season, developmental stage and species.

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