ECOLOGY LETTERS 〔cnrs〕 WILEY

High intraspecific growth variability despite strong evolutionary legacy in an Amazonian forest

Sylvain Schmitt[1,2,3] ⓘ | Bruno Hérault[3,4,5] ⓘ | Géraldine Derroire[6] ⓘ

[1]CNRS, UMR EcoFoG (Agroparistech, Cirad, INRAE, Université des Antilles, Université de la Guyane), Kourou, French Guiana

[2]CIRAD, UPR Forêts et Sociétés, Montpellier, France

[3]Forêts et Sociétés, Univ Montpellier, CIRAD, Montpellier, France

[4]CIRAD, UPR Forêts et Sociétés, Yamoussoukro, Côte d'Ivoire

[5]Institut National Polytechnique Félix Houphouët-Boigny, INP-HB, Yamoussoukro, Côte d'Ivoire

[6]Cirad, UMR EcoFoG (Agroparistech, CNRS, INRAE, Université des Antilles, Université de la Guyane), Kourou, French Guiana

Correspondence
Sylvain Schmitt, UMR EcoFoG, Campus Agronomique, 97310 Kourou, French Guiana.
Email: sylvain.m.schmitt@gmail.com

Editor: Jelena H. Pantel

Abstract

Tree growth is key to species performance. However, individual growth variability within species remains underexplored for a whole community, and the role of species evolutionary legacy and local environments remains unquantified. Based on 36 years of diameter records for 7961 trees from 138 species, we assessed individual growth across an Amazonian forest. We related individual growth to taxonomy, topography and neighbourhood, before exploring species growth link to functional traits and distribution along the phylogeny. We found most variation in growth among individuals within species, even though taxonomy explained a third of the variation. Species growth was phylogenetically conserved up to the genus. Traits of roots, wood and leaves were good predictors of growth, suggesting their joint selection during convergent evolutions. Neighbourhood crowding significantly decreased individual growth, although much of inter-individual variation remains unexplained. The high intraspecific variation observed could allow individuals to respond to the heterogeneous environments of Amazonian forests.

KEYWORDS
forest gap dynamics, functional traits, Paracou, phylogeny, topography, tree growth

INTRODUCTION

Individual growth is a key determinant of species performance (Violle et al., 2007) and a driver of forest dynamics (Herault et al., 2010) and composition (Russo et al., 2008). Thus, a comprehensive understanding of the determinants of tree growth is of primary importance for predicting the fate of tropical forests. Tree growth plays a major role in the ecological strategies of tree species through demographic trade-offs (Rüger et al., 2020). For instance, the growth-mortality trade-off opposes fast- to slow-growing species (Aubry-Kientz et al., 2015a; Philipson et al., 2014), with lower support costs but at greater risk of damage and increased mortality (King et al., 2006). To forecast the dynamics of tropical forests, efforts have been made to

predict the growth of species, notably using functional traits (Hérault et al., 2011; Osazuwa-Peters et al., 2017). Functional traits, defined as phenotypic traits that have an impact on fitness through their effect on individual performance (Violle et al., 2007), are expected to play a role in species growth (but see Yang et al., 2018). For instance, wood density has been shown to be an important determinant of species growth potential (Hérault et al., 2011; King et al., 2005; King et al., 2006; Visser et al., 2016), as well as species maximum diameter and height, (Hérault et al., 2011), wood anatomical features (Osazuwa-Peters et al., 2017) and hydraulic conductance (Poorter et al., 2010).

Multiple environmental determinants of species growth have been identified, which in turn affect species distribution. Light availability was recognized

early on as a key factor in the growth of species at different life stages (Baraloto et al., 2005; King et al., 2005). Fast-growing species are found in environments with high access to light, where shade-tolerants show reduced growth (Wright et al., 2010). Treefalls open gaps with bright environments and reduced competition. During forest succession, gaps are closing, resulting in shadier environments and increased competition. This process, called forest gap dynamics (Martinez-Ramos et al., 1989), produces successional niches, favouring species with a variety of survival and growth strategies (Herault et al., 2010; Rüger et al., 2011). Fast-growing pioneer species quickly colonize gaps, while slower-growing late-successional species gradually establish themselves in shadier environments (Craven et al., 2015). Nutrient and soil water availability also shape species performance with fast-growing species dying more on the poorest habitat and slow-growing species being outcompeted in resource-rich habitats (Russo et al., 2008).

The functional traits used to study species strategies are however still poor predictors of individual tree rates (Yang et al., 2018), partly because they ignore individual variation, and because critical aspects of demographic rates are not captured by most measured functional traits. Individual- and species-based approaches to functional traits are conceptually different (Poorter et al., 2018): the species-based approach focuses on potential while the individual-based approach focuses on realized traits and rates. Individual growth rates depend on access to resources, which are modulated by biotic interactions with neighbouring trees. Two environmental drivers can capture these interacting effects. (1) Topography is driving both water and nutrient availability in tropical forests (Ferry et al., 2010; John et al., 2007), resulting in individual growth within species faster in bottomlands than on ridges in Amazonian forests (Fortunel et al., 2018; but see O'Brien & Escudero, 2021). (2) Neighbourhood crowding through competition for resources, including light, nutrients and water, is known to modulate tree growth (Lewis & Tanner, 2000; Uriarte et al., 2004a). Individuals' responses to neighbourhood crowding depend on the species identity of the focal tree and the composition of its neighbours (Lewis & Tanner, 2000; Uriarte et al., 2004b). Neighbourhoods interact with other abiotic factors, e.g. growth is faster in bottomland than on higher ground, but neighbourhood crowding has a stronger negative effect on growth in bottomland (Fortunel et al., 2018). Neighbourhood crowding also captures the effect of forest gap dynamics, which is a key factor shaping the growth of individuals within species with increased tree growth near canopy openings (Herault et al., 2010; Schmitt et al., 2022).

Most of the studies of intraspecific variation in growth were carried out for a limited number of species of a community. This prevents assessing the relative contribution to individual growth variability of species

evolutionary legacy, individual adaptations and individual plasticity in response to local environments. We define evolutionary legacy as the contribution of phylogenetic relatedness to species phenotypic variation, following Coelho de Souza et al., 2016, which is linked to phylogenetic background composed of both species genetic drift and adaptations. Individual trees however differ in many dimensions within and among species that may influence their growth response to local abiotic environments and biotic interactions (Le Bec et al., 2015). Genetic processes within and among species hold promises for understanding tree growth (Grattapaglia et al., 2009). Evolutionary legacy resulted in convergent species growth within tree genera from the Amazon Basin (Coelho de Souza et al., 2016). A recent study further suggested individual adaptation of tree growth within species to the successional niches generated by tropical forest gap dynamics in the tropical species from the *Symphonia* genus (Schmitt et al., 2022). The topographic origin of parent trees was also shown to determine the individual's growth response of the offspring to increasing abundance of neighbours (O'Brien Escudero, 2021). Altogether these results plead for a better integration of species and individuals in tree growth studies, in order to better link individual tree growth to genetic, phylogenetic and environmental variations.

Here, we assessed tree growth potential for most individuals in a local Amazonian forest community, and related variation in individual growth potential to taxonomy, topography and neighbourhood crowding, in addition to the species phylogeny. Based on 36 years of diameter records for 7961 trees belonging to 138 species, we constructed individual growth trajectories and inferred individual growth potential using a hierarchical Bayesian model. We used individual growth potential in a linear mixed model with topography, neighbourhood crowding and taxonomy to explore the environmental drivers and evolutionary legacy of tree growth. We further explored the phylogenetic signal of species growth potential and the role of functional traits in explaining species growth potential. We specifically addressed the following questions:

1. What is the importance of evolutionary legacy in the growth potential of tropical trees?
2. Can functional traits help predict species growth potential?
3. How important is the variability of individual growth potential within species, as compared to the variability at other taxonomic levels, and how does the local environment influence it?

We hypothesized species growth to show a phylogenetic signal with conserved interspecific growth in part influenced by species functional traits. We expected high intraspecific variation in tree growth influenced by topography and neighbourhood crowding.

MATERIALS AND METHODS

Study site

The study was conducted in the coastal region of French Guiana, at the Paracou field station (5°18′ N, 52°53′ W). The site is characterized by an average annual rainfall of 3041 mm and an average air temperature of 25.71°C (Aguilos et al., 2018). A rich tropical forest occupies this lowland area characterized by heterogeneous microtopographic conditions with numerous small hills (Gourlet-Fleury et al., 2004). The site includes 15 6.25 ha plots and a 25 ha plot with trees mapped to the nearest metre and censused (diameter at breast height >10 cm) every 1–5 years since 1985. Nine of the plots were intentionally manipulated in 1986 with a range of disturbance intensities that created a variety of biotic environments (Hérault & Piponiot, 2018).

Species and individuals

We focused on trees located 20 m from any plot edge for neighbourhood analyses. We used only (i) trees recruited since the beginning of censuses to exclude large diameter trees that show little to no variation in their growth trajectories, (ii) trees with at least 10 measurements to better assess their complete growth trajectories and (iii) species with at least 10 trees meeting the previous requirements for a good representation of intraspecific variability. We did include disturbed plots in our study in order to explore a greater variety of neighbourhood crowding.

Individual growth

We first used a reduced dataset to explore the best model shape (Table S1) and the best hierarchical integration of individual and species effects (Table S2) to infer individual growth potential. Based on goodness of fit (likelihood), cross-validation (leave-one-out estimate of the expected log pointwise predictive density, see Vehtari et al., 2017) and prediction quality (root mean square error of prediction), we chose to model the diameter $DBH_{i,t}$ of individual tree i at census t using a Gaussian distribution centred on the sum of the arithmetic series of the annual tree growth rate (model 1). $DBH_{i,t}$ can be calculated as previous year individual diameter $DBH_{i,t-1}$ plus individual annual growth rate $AGR_{i,t}$:

$$DBH_{i,t} = DBH_{i,t-1} + AGR_{i,t} \qquad (1a)$$

This arithmetic series can be integrated from individual recruitment to build individual growth trajectory to annual individual diameter $DBH_{i,t}$:

$$DBH_{i,t} = DBH0_i + \sum_{y=0}^{y=t} AGR_{i,y} \qquad (1b)$$

where $DBH0_i$ is individual diameter at recruitment.

At any year t since tree recruitment, individual annual growth rate $AGR_{i,t}$ can be obtained following a Gompertz model (Hérault et al., 2011) based on individual diameter at breast height from previous census $DBH_{i,t-1}$:

$$AGR_{i,t} = Gmax_i \times \exp\left(-\frac{1}{2} \left[\frac{\log(DBH_{i,t-1}/Dopt_i)}{Ks_i} \right]^2 \right) \qquad (1c)$$

where $Gmax_i$ is the individual maximum growth potential, $Dopt_i$ is the optimal diameter at which the individual reaches its maximum growth potential, and Ks_i is the kurtosis defining the width of the bell-shaped growth-trajectory (see figure 1 in Hérault et al., 2011).

Resulting from equations (Equation 1a, 1b and 1c), model 1 can be written so that diameter $DBH_{i,t}$ of individual i at time t is modelled with observed diameters from previous censuses:

$$DBH_{i,t} \sim N\left(DBH0_i + \sum_{y=0}^{y=t} Gmax_i \times \exp\left(-\frac{1}{2} \left[\frac{\log(DBH_{i,t-1}/Dopt_i)}{Ks_i} \right]^2 \right), \sigma \right) \qquad (model\ 1)$$

$Gmax_i$ is a fixed effect, while $Dopt_i$ and Ks_i are random effects centred on species parameters $Dopt_s$ and Ks_s with associated variances σD and σK.

This model was fitted for every census t at which the individual was measured. A Bayesian method was employed to infer parameters using the stan language (Carpenter et al., 2017) and the *rstan* package (Stan Development Team, 2018) in the R environment (R Core Team, 2020).

Descriptors of individual growth potential

We used the mean neighbourhood crowding index (NCI, Uriarte et al., 2004a, b) over the last 30 years, an indirect measurement of access to light and forest gap dynamics. The mean neighbourhood crowding index NCI_i from tree individual i was calculated as follows:

$$NCI_i = \overline{\sum_{j\,|\,\delta_{i,j}<20m} DBH_{j,t}^2 \times \exp\left(\frac{-1}{4}\delta_{i,j} \right)}$$

with $DBH_{j,t}$ the diameter of the neighbouring tree j in year t and $\delta_{i,j}$ its distance to the individual tree i. NCI_i is computed for all neighbours at a distance $\delta_{i,j}$ inferior to the

maximum neighbouring distance of 20 m. The power of neighbours' $DBH_{j,t}$ effect was set to 2 to represent an area. The decrease of neighbours' diameter effect with distance was set to $-\frac{1}{4}$ to represent trees at 20 m of the focal trees having less than 1% of the effect of the same tree at 0 m (i.e. $\exp(-\frac{1}{4} \times 20) < 1\%$). NCI_i is computed as the mean of $NCI_{i,t}$ per census over the last 30 years denoted by the overline in the equation.

We used the topographic wetness index (TWI) as proxy of the distribution of soil water and nutrients in Paracou (Schmitt, Tysklind, Hérault, & Heuertz, 2021). Waterlogging and topography have been highlighted as crucial for forest dynamics (Ferry et al., 2010), species-habitat relationships (Engelbrecht et al., 2007), and phenotypic variation (Schmitt, Hérault, et al., 2020). TWI was derived from a 1-m-resolution digital elevation model using SAGA-GIS (Conrad et al., 2015) based on a LiDAR campaign of the whole Paracou field station done in 2015.

We also tested the link between functional traits and species growth using the mean trait values of the 120 species that Vleminckx et al. (2021) shared with our study (over the 138 species available, Figure S10). Vleminckx et al. (2021) functional data included 19 leaf, stem and root traits.

Analyses

To study the effect of phylogeny and environment, we investigated the effects of family, genus, species, topography (TWI) and neighbourhood (NCI) indices on individual growth potential (Gmax) modelled using model 1 with a linear mixed model (model 2). Environmental variables (TWI and NCI) were used as fixed effects, while taxonomic levels (family, genus and species) were used as random effects. We propagated the uncertainty in the estimation of individual growth (model 1) to the model testing the effect of phylogeny and environment (model 2). To do so, we considered the individual growth potentials obtained in 500 iterations of model 1 as 500 different dataset on which we fitted a Bayesian linear mixed model (model 2). For each of these dataset, we kept the 1000th iteration after a warm up of 999 iterations. We pooled all these last iterations to obtain a posterior distribution of the effect of phylogeny and environment that takes into account the uncertainty in individual growth potential. We reported the resulting marginal (fixed effects alone) and conditional (fixed and random effects) goodness of fit (R^2, Nakagawa & Schielzeth, 2013).

We further investigated species growth potential across the phylogeny binding the Paracou species to the backbone phylogeny of two recently published megatrees (Smith & Brown, 2018; Zanne et al., 2014) using the *V.PhyloMaker* R package (Jin & Qian, 2019). To account for the lognormal distribution of individual growth

potential within species (Schmitt et al., 2022), we used the median as a measure of species growth potential ($Gmax_s = \text{Median}(Gmax_i)$). We tested the phylogenetic signal of species growth potential with multiple measures including Pagel's λ (Keck et al., 2016).

We finally explored the link between species functional traits and species growth potential. We used a multimodels inference explaining species log-transformed growth potential with log-transformed functional traits to meet the normality assumptions with all combinations of the 18 functional traits using the *glmulti* R package (Calcagno & de Mazancourt, 2010). We used Buckland et al. (1997)s approach to weight variables by Akaike Information Criterion (AIC) and summarized their estimates, confidence and importance. We further used the best model inference according to AIC to compute the *p*-value and R^2 contribution averaged over orderings of regressors as in Lindeman, Merenda and Gold (1980), using the function *relimp* from the *relaimpo* R package (Groemping 2006). In parallel, we used boosted regression trees (BRT) to infer functional traits relative information in explaining species growth potential using the *gbm* R package (Greenwell et al., 2022) with 10,000 trees containing at least five observations per node and a shrinkage of 5×10^{-4} after model tuning. We used the *tidyverse* (Wickham et al., 2019), *lme4* (Bates et al., 2015), *phylosignal* (Keck et al., 2016) and *ggtree* (Yu, 2020) packages in the R environment (R Core Team, 2020) for all analyses.

RESULTS

We recorded 117,688 diameter measurements in the local community across 7961 individuals belonging to 138 species, 95 genera and 38 families. Bayesian inference of the individual growth model converged correctly (e.g., Figure S1) with a good mixture of chains for most of the individual growth potentials ($Gmax_i$) shown with an $\widehat{R} < 1.1$ (99.2%, Figure S2). The posteriors of the parameters did not show any correlation problems (e.g., Figure S3). Posterior distributions of individual growth potentials showed limited uncertainty (e.g., Figure S4). The resulting predicted diameters showed very high goodness of fit with a root mean square error of 0.43 cm (Figure 1, illustrated for 90 individuals in 9 species in Figure S5). Species median values of growth potential ranged from 0.34 to 4.50 cm per year with a coefficient of variation from 0.25 to 1.78 cm per year (Table S5).

Based on the infer-red individual growth potentials, we found most of the variation in growth potential to be among individuals within species shown with residuals ($\sigma = 0.72$, Table 1), then among genera within families ($\sigma = 0.12$), then among species within genera ($\sigma = 0.04$) and among families ($\sigma = 0.03$). The taxonomic structure explained about a third of the observed variation in individual growth potential (Conditional

RMSE = 0.43 cm
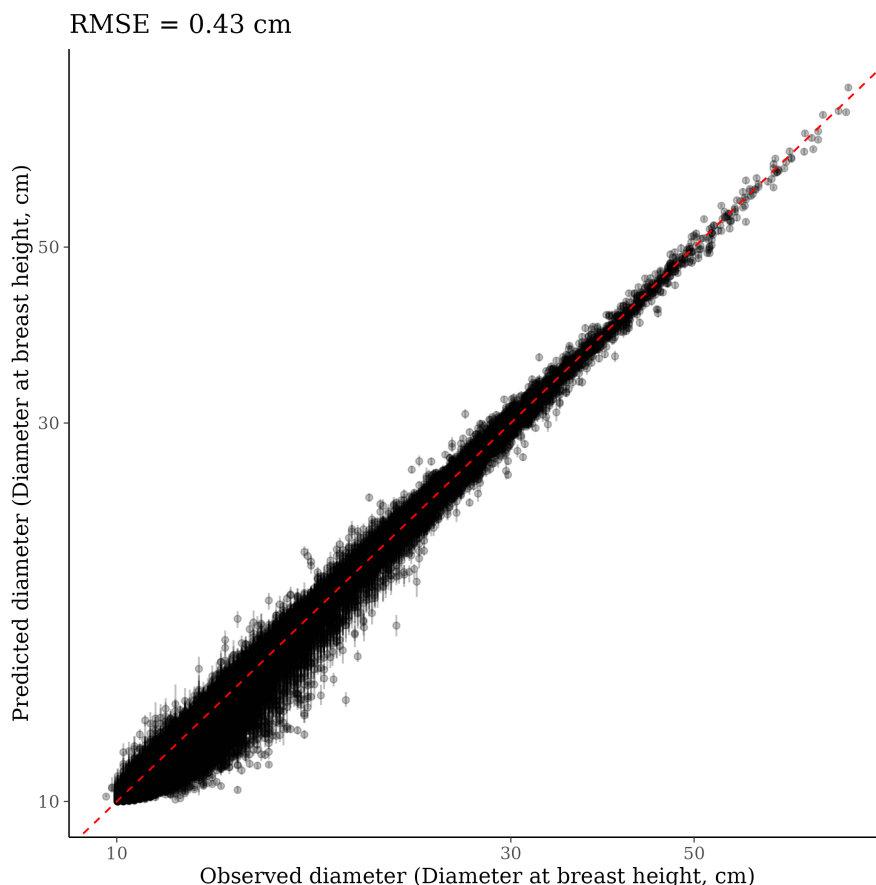
FIGURE 1 Goodness of fit for Bayesian inference of the individual growth model, illustrated by predicted versus observed diameters at breast height. The dots represent the median of the posterior distributions of predicted diameters while the error bars show the 90% credibility intervals. The red-dashed line represents the expected value for a perfect prediction (1:1). The X and Y axes have been log-transformed to better represent the many small diameter values. An example of corresponding diameter trajectories can be found in Figure S4.

$R^2 = 0.347$ against Marginal $R^2 = 0.019$). The neighbourhood crowding index (NCI) had a marked negative significant effect on individual growth potential ($\beta = -0.51, \text{CI} = [-0.61; -0.42]$, Table 1, Figure 2a; Figure S6) which explained 2% of the observed variation knowing taxonomy (Marginal $R^2 = 0.019$, Table 1). The topographic wetness index had no effect on individual growth potential ($\beta = -0.03, \text{CI} = [-0.13; 0.07]$, Table 1; Figure S6). The model residuals showed no spatial autocorrelation (Figure S11).

Species growth potential was significantly structured in the phylogeny (Pagel's $\lambda = 0.78, p < 0.001$, Figure 2b; Table S3). Phylogenetic autocorrelograms revealed a short distance significant positive association and a long distant significant negative association of species growth potential in the phylogeny (Figure S7). The local indicator of phylogenetic association highlighted the conservation of species growth potential at the genus level (Figure S8), as illustrated with fast-growing species from the *Cecropia* genus opposed to slow-growing species from *Eschweilera* (Figure 2c). However, a few species have different growth potential in the same genus, such as slow growing *Drypetes variabilis* opposed to fast growing *Drypetes fanshawei*.

Functional traits explained 40% of the observed variation of species growth potential among 120 tropical tree species ($R^2 = 0.409$). Sapwood-specific gravity, fine roots diameter and leaf calcium content had significant negative effects on species growth potential, while leaf nitrogen content had a significant positive effect (Table 2). Sapwood-specific gravity and leaf nitrogen content had the largest importance (multimodels importance >0.93, BRT relative information >17% and best models $R^2 > 0.09$), while other traits had smaller importance (relative information <8% and best models $R^2 \leq 0.03$). Fine root diameter has a multimodels importance of 0.99, meaning that it was retained in most regressions, but a relatively low relative information of 4.22% associated with a low R^2 of 0.03, indicating that the variable increases the overall information of the model (AIC) but provides little information on the response variable.

DISCUSSION

Using 36 years of diameter records for 7961 trees from 138 species, we found that the evolutionary legacy of species shaped individual growth trajectories, explaining up to

TABLE 1 Effects of phylogeny and environment on individual growth potential.

$\log(G\mathrm{max}_i)$		
Predictors	Estimates	CI (95%)
Intercept	3.88	3.05 to 4.68
$\log(\mathrm{NCI}_i)$	−0.51	−0.61 to −0.42
$\log(\mathrm{TWI}_i + 1)$	−0.03	−0.13 to 0.07
Random effects		
Residual (Individual)	0.72	
Species|Genus|Family	0.04	
Genus|Family	0.12	
Family	0.03	
Marginal R^2/Conditional R^2	0.019/0.347	

Note: We investigated the effects of family, genus, species, topography (TWI) and neighbourhood crowding (NCI) indices on individual growth potential ($G_{\max}$) with a linear mixed model. First rows show estimates and credible intervals (CI) for environmental fixed effects. Middle rows show estimates for variance components from phylogenetic random effects. The last row shows marginal (fixed effects alone) and conditional (fixed and random effects) goodness of fit.

one-third of the observed variation in growth potential among the eight thousand individuals studied. Functional traits of wood, leaves and roots together predicted species growth potential, showing that multiple functional dimensions determine the performance of tropical tree species in their environments. Phylogenetic correlograms suggested joint selection of species' growth strategies and associated functional traits during convergent evolutions. Nevertheless, at the individual tree level, the observed effect of neighbourhood crowding suggests that forest gap resulted in fast-growing trees in high light conditions with reduced competition, as opposed to slow-growing trees in low light conditions with strong competition. But the ecological and evolutionary drivers of the high variability in individual growth potential remain largely undetermined, and the underlying factors, which include phenotypic plasticity and genetic adaptations, are little explored. The high intraspecific variation observed could allow individuals in hyperdiverse ecosystems such as tropical forests to respond to the variable light and competitive conditions offered by successional niches during forest gap dynamics, in addition to the many other potential environmental dimensions that shape the coexistence of species.

Evolutionary legacy shapes the growth of tropical trees

We found that evolutionary legacy shaped individual growth potential. Previous studies already highlighted regionally a phylogenetic signal in species growth potential in the Amazon Basin, with evolutionarily related genera having more similar growth values than expected by chance (Coelho de Souza et al., 2016). Regionally, woody biomass and tree size also showed a strong phylogenetic signal in tropical dry forests (de Aguiar-Campos et al., 2021), besides longevity rather than growth determined biomass (Körner, 2017). Similarly, Cadotte et al. (2009) found evolutionary relationships explaining grasslands productivity. Thus, evolutionary legacy shapes observed phylogenetic and functional diversity at the regional scale, with for instance lasting influences from the Paleoclimate (Bosela et al., 2016; Svenning et al., 2015). Our results are in agreement as we identified a strong phylogenetic signal in species growth potential with positive phylogenetic correlation up to the genus level, showing that previous regional scale results hold locally. Using taxonomy as a proxy, we found that the evolutionary legacy of species explained up to one-third of the observed variation in growth potential among the eight thousand individuals studied.

Several convergent evolution events resulted in similar growth patterns of species within genera with, for instance, repeated evolution of fast-growing species in Urticaceae, Fabaceae, Hypericaceae and Melastomataceae families with species, respectively, belonging to the *Cecropia*, *Inga*, *Vismia* and *Miconia* genera. This pattern might be explained by repeated evolution constrained by forest gap dynamics, leading to shade-tolerance under closed canopies as opposed to fast-growing pioneer species in light gaps (Coelho de Souza et al., 2016). Indeed, *Cecropia, Visimia* and *Miconia* are, for instance, recognized as pioneer species colonizing first light gaps after a treefall (Dalling et al., 1998). Convergent evolutions of habitat specialization could also explain the divergent growth of genera within families. For instance at the species level, Fine et al. (2014) evidenced specialization to white sands or flooded soils within *Protieae*. Nevertheless, the fact that topography and forest gap dynamics, two major determinants of the local community (e.g. Ferry et al., 2010; Molino & Sabatier, 2001), have less explanatory power than taxonomy reveals the importance of past evolutionary constraints on the growth trajectories of individual trees through species legacy compared to the direct effect of the current environment to which individual trees could respond through microadaptations and phenotypic plasticity (e.g. Schmitt et al., 2022; Schmitt, Tysklind, Hérault, & Heuertz, 2021).

Taken together, our results, therefore, partly support species-averaged community ecology approaches, at least for growth trajectories (but see last paragraph). Swenson (2013) suggested the use of phylogenetic approaches to understand community assembly, although they are insufficient to predict demographic rates (Che-Castaldo et al., 2018) given the high remaining intraspecific variability and differences observed among closely related species.

Multiple functional dimensions together predict the species growth potential

Using the 120 species in common with Vleminckx et al. (2021), we found few functional traits explaining an
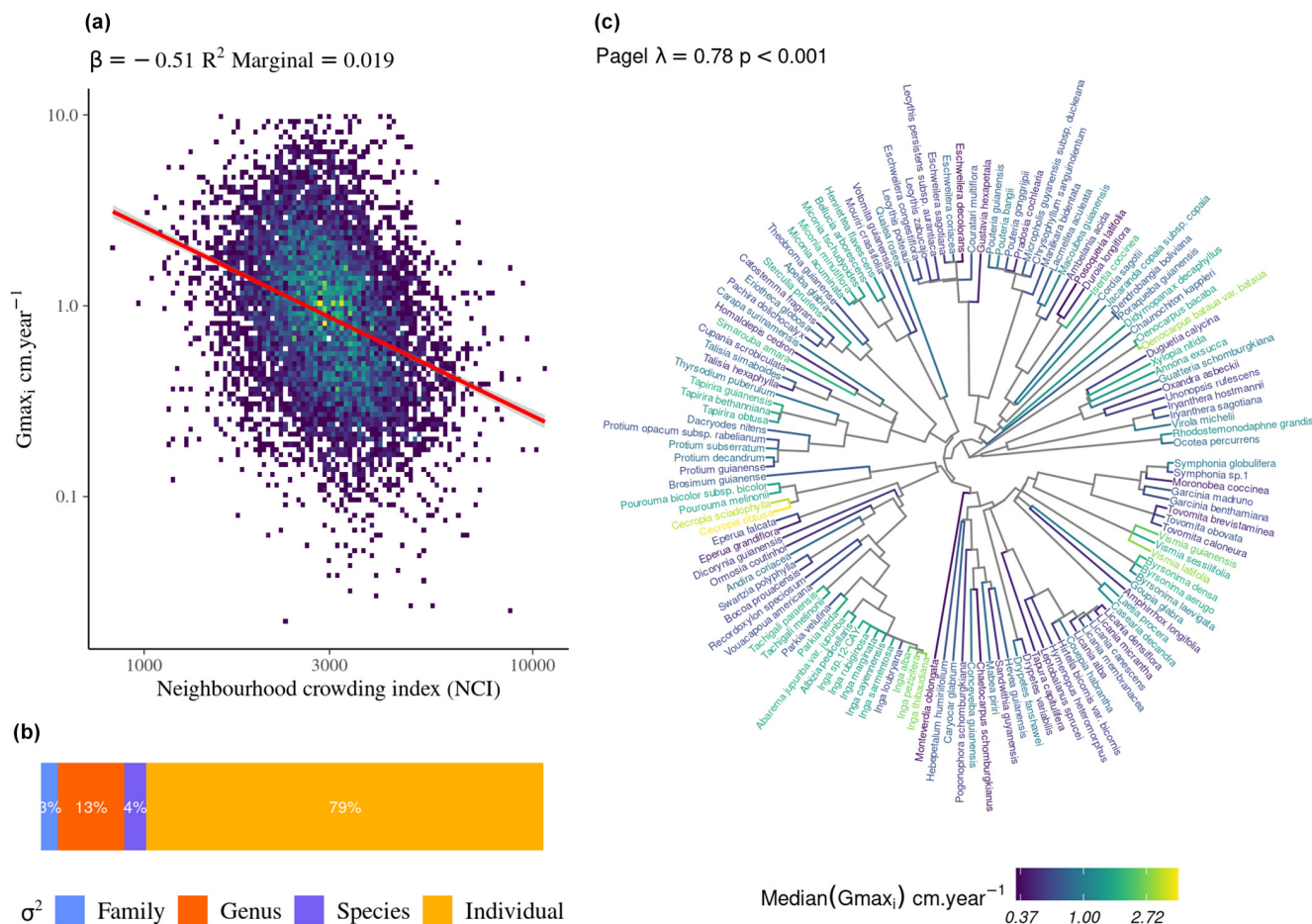
FIGURE 2 Variation in the growth potential of individuals and species as a function of neighbourhood crowding, taxonomic levels or across phylogeny. (a) Individual growth potential ($Gmax_i$) is significantly decreasing with neighbourhood crowding index (NCI, $\beta = -0.51$, Marginal $R^2 = 0.019$, see Table 1). (b) The partitioning of the variation of individual growth potential ($Gmax_i$) across taxonomy shows that most of the variation occurs at the individual ($\sigma = 0.72$, Table 1), then genus ($\sigma = 0.12$) before species ($\sigma = 0.04$) and family ($\sigma = 0.03$) levels. (c) The distribution of species growth potential (Median[$Gmax_i$]) across the phylogeny from slow growing species in dark blue to fast growing species in yellow (log-scale) is phylogenetically structured (Pagel's $\lambda = 0.78$, $p < 0.001$) with a significant positive autocorrelation to a phylogenetic partistic distance below 100 (Figure S1), corresponding to the genus level (Table 1).

important part of variation in species growth potential (40%). Sapwood-specific gravity was already shown to be a major predictor of species growth (Hérault et al., 2011; King et al., 2005; King et al., 2006; Visser et al., 2016), with fast-growing species investing less in wood resulting in a low density as opposed to slow-growing ones. Leaf nitrogen content was the second-most important predictor in our study, with nitrogen-rich species growing faster, as already observed for pioneer species (Aidar et al., 2003), and in rich environments (Russo et al., 2008). Finally, root traits also predicted species growth potential with fast-growing species investing less in their root systems with decreased fine roots diameters, as already shown for temperate species (Comas et al., 2002; Comas & Eissenstat, 2004) but not in the tropics. Soil heterogeneity can be expected to play a key role in shaping root traits (Vleminckx et al., 2021), while the dynamics of forest gaps cannot be excluded either (Xiang et al., 2013).

Future research on the role of root traits in tropical tree growth is thus particularly promising given that

tropical forests harbour the greatest diversity of root characteristics (Ma et al., 2018). Interestingly, species growth potential is better predicted by the combination of traits from roots, wood and leaf, in accordance with the idea of multiple functional dimensions that allow tropical tree species to optimize their performance in a given environment (Vleminckx et al., 2021), while participating together in a whole plant economic spectrum (Reich, 2014).

Finally, we found a similar phylogenetic structure between the functional traits and species growth potential (Figure S9), with significant and positive phylogenetic correlation at short distance, in particular in sapwood-specific gravity (Coelho de Souza et al., 2016). The traits explaining the most species growth had the strongest positive phylogenetic correlation. The similarity between phylogenetic correlograms suggests a joint selection of species growth strategies and associated functional traits during convergent evolutions.

TABLE 2 Effects of functional traits on species growth potential. We extracted traits from Vleminckx et al. (2021) for the 120 species shared with our study.

log(Gmax$_s$)

Predictors	Multimodels inference			Boosted regression trees	Best model inference	
	Estimates	Confidence	Variable Importance	Relative information	p-Value	R^2
Intercept	−0.78	2.87	1			
Sapwood-specific gravity	**−1.37**	**0.48**	**1**	**17.67**	**<0.001**	**0.21**
Fine roots diameter	**−0.73**	**0.64**	**0.99**	**4.22**	**0.005**	**0.03**
Leaf calcium content	**−0.12**	**0.13**	**0.95**	**6.72**	**0.008**	**0.02**
Leaf nitrogen content	**0.52**	**0.44**	**0.93**	**23.47**	**<0.001**	**0.09**
Roots wood-specific gravity	0.1	0.25	0.49	1.76	0.070	0.01
Specific root tip abundance	−0.07	0.18	0.47	4.25		
Specific root length	−0.09	0.26	0.45	4.19	0.055	0.03
Chlorophyll content	0.15	0.42	0.41	0.88	0.162	0.01
Trunk bark thickness	−0.06	0.17	0.39	7.09		
Leaf thickness	−0.08	0.29	0.2	0.9		
Fine roots tissue density	−0.01	0.06	0.08	9.5		
Leaf phosphorus content	0	0.02	0.07	3.49		
Leaf carbon content	−0.03	0.29	0.07	1.06		
Specific leaf area	−0.01	0.04	0.06	0.91		
Leaf potassium content	0	0.02	0.06	3.99		
Leaf toughness	0	0.02	0.06	2.38		
Leaf area	0	0.01	0.06	7.5		
R^2/R^2 adjusted					0.409 / 0.370	

Note: We used both multimodels inference using all linear combinations from the 18 log-transformed functional traits and boosted regression trees with 10,000 trees containing at least five observations per node. Columns show multimodels averaged estimates, confidence and variable importance; boosted regression trees relative information, and best model inference significance (p-value) and relative importance (R^2). The last row shows raw and adjusted goodness of fit for the best model inference. Functional traits with a variable importance above 0.5 and relative information above 10% are shown in bold.

Individual growth potential is influenced by forest gap dynamics but remains largely unexplained

We found evolutionary legacy shaping the individual growth of tropical trees, with functional traits as important predictors of species growth potential. However, we still observe a huge intraspecific variation with individual growth potential varying widely within species (logarithmic coefficient of variation of 98% [35–430%]). The growth trajectories of individual trees are strongly and negatively affected by the average neighbourhood crowding over the last 30 years, which can be related to the mosaic of light and competition environments shaped by forest gap dynamics (Schmitt et al., 2022). In a nutshell, we observe fast-growing trees in high-light conditions with decreased competition opposed to slow-growing trees in low-light conditions with strong competition within and among species. Fast-growing pioneer species opposed to slow-growing species under closed-canopies are widely known and expected at the interspecific level (Dalling et al., 1998; Hérault et al., 2011; King et al., 2005; Molino & Sabatier, 2001), but we also evidenced fast-growing individual opposed to slow-growing individual within species along successional niches, advocating for a wide breadth of successional niches in tropical tree species (e.g. Schmitt et al., 2022). The effect of competition and its reduction has already been suggested as a factor increasing tree radial growth within species in the context of selective logging, especially within shade-tolerant species (Peña-Claros et al., 2008). Indeed, logging gaps, with increased light access, results in increased tree growth at short distance from the gap, especially within slow-growing species (Herault et al., 2010). The effect of crowding can be a direct limit to light access expected in successional niches, but the effect of neighbours identity found in tropical trees (Potvin & Gotelli, 2008) also suggests other above- and below-ground competition and facilitation processes. In short, forest gap dynamics with tree fall results in successional niches ranging from high light and low competition with fast-growing trees and species after recent tree fall to low light and high competition with slow-growing ones in closed canopies.

Nevertheless, forest gap dynamics only explained a tenth of the high variation of individual growth potential within species. Topographic position, proxied with

topographic wetness index, did not influence the individual growth variation within species in our study (but see O'Brien & Escudero, 2021), despite its known importance in tropical forest dynamics (Ferry et al., 2010). The role of topography on individual growth potential was weak, but we can assume that topography shapes species growth through species evolutionary legacy, as several species studied showed locally pervasive habitat preferences along topography (Allié et al., 2015; Schmitt, Tysklind, Derroire, et al., 2021) and microgeographic adaptations to topography (Schmitt, Tysklind, Hérault, & Heuertz, 2021). Consequently, ecological and evolutionary factors of individual growth potential remain largely undetermined. The process through which forest gap dynamics and undetermined factors affect individual growth potential also remains underexplored. The spatio-temporal variation of forest gap dynamics led to assume growth potential variation within species to be due to phenotypic plasticity (dos Santos & Ferreira, 2020). However, recent studies revealed local adaptation (O'Brien & Escudero, 2021) and microadaptation (Schmitt et al., 2022) of individual trees within species to neighbourhood crowding and competition resulting in varying individual growth potential. Thus, forest gap dynamics could have both a strong evolutionary legacy on species and may shape genotypes within species with strong spatio-temporal variations (Schmitt et al., 2022).

Intraspecific variability in performance can have strong implications for species coexistence (Chesson, 2000; Clark, 2010; Stump et al., 2022), although this view remains an open question (Clark et al., 2022). Clark (2010) suggested that intraspecific variability allows species to differ in the distribution of their responses to the environment and thus to pass environmental filtering: an individual may persist in a given environment with a suitable phenotype while the same environment would have filtered out the average phenotype of the species. This hypothesis is consistent with theories that predict the coexistence of a greater number of species, with competition being stronger within species, among individuals, than among species (Chesson, 2000). Modelling approaches further support the hypothesis that intraspecific genetic and phenotypic variability promotes species coexistence (Lichstein et al., 2007). In the case of forest gap dynamics, late-successional species have been shown to have more variation in response to competition and light variation than early-successional species (Herault et al., 2010; Peña-Claros et al., 2008), which could be linked to a greater diversity of light and competitive environments. The high intraspecific variation observed could therefore allow individuals to adjust to the variable conditions of light and competition offered by the successional niches during the closure of the forest gaps, in addition to the other numerous potential niches shaping the high-dimensional coexistence of species (Clark, 2010). Consequently, the methodology used in our study paves the way to future research on

determinants and processes shaping tree growth within and among species. The combination of studies from forest censuses (this study), modelling approaches (Schmitt, Maréchaux, et al., 2020) and experimental studies (O'Brien & Escudero, 2021) holds promise for a better understanding of tree performance within and among species, with the potential to better explain and predict species coexistence and forest dynamics. In particular, linking individual genotypes within species to forest gap dynamics, topography and individual growth potential (Schmitt et al., 2022) among several species to extrapolate to the community level seems a promising approach to elucidate the determinants of tree growth.

CONFLICT OF INTEREST STATEMENT
The authors declare they have no conflict of interest relating to the content of this article.

PEER REVIEW
The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ele.14318.

DATA AVAILABILITY STATEMENT
DBH and spatial positions of individuals were extracted from the Paracou Station database, for which access is available at https://dataverse.cirad.fr/dataverse/paracou with corresponding DOIs given in Table S4 (DOIs:10.18167/DVN1/NSCWF0; 10.18167/DVN1/Q8V2YI; 10.18167/DVN1/LIVCEK; 10.18167/DVN1/HWTD4U; 10.18167/DVN1/HIGNWQ). Scripts used for analyses can be found on GitHub (https://github.com/sylvainschmitt/treegrowth).

ORCID
Sylvain Schmitt https://orcid.org/0000-0001-7759-7106
Bruno Hérault https://orcid.org/0000-0002-6950-7286
Géraldine Derroire https://orcid.org/0000-0001-7239-2881

REFERENCES
Aguilos, M., Stahl, C., Burban, B., Hérault, B., Courtois, E., Coste, S. et al. (2018) Interannual and seasonal variations in ecosystem

transpiration and water use efficiency in a tropical rainforest. *Forests*, 10(1), 14. Available from: https://doi.org/10.3390/f10010014

Aidar, M.P.M., Schmidt, S., Moss, G., Stewart, G.R. & Joly, C.A. (2003) Nitrogen use strategies of neotropical rainforest trees in threatened Atlantic Forest. *Plant, Cell and Environment*, 26(3), 389–399. Available from: https://doi.org/10.1046/j.1365-3040.2003.00970.x

Allié, E., Pélissier, R., Engel, J., Petronelli, P., Freycon, V., Deblauwe, V. et al. (2015) Pervasive local-scale tree-soil habitat association in a tropical forest community. *PLoS One*, 10(11), e0141488. Available from: https://doi.org/10.1371/journal.pone.0141488

Aubry-Kientz, M., Rossi, V., Boreux, J.-J. & Hérault, B. (2015a) A joint individual-based model coupling growth and mortality reveals that tree vigor is a key component of tropical forest dynamics. *Ecology and Evolution*, 5(12), 2457–2465. Available from: https://doi.org/10.1002/ece3.1532

Aubry-Kientz, M., Rossi, V., Wagner, F. & Hérault, B. (2015b) Identifying climatic drivers of tropical forest dynamics. *Biogeosciences*, 12(19), 5583–5596. Available from: https://doi.org/10.5194/bg-12-5583-2015

Baraloto, C., Goldberg, D.E. & Bonal, D. (2005) Performance trade-offs among tropical tree seedlings in contrasting microhabitats. *Ecology*, 86(9), 2461–2472. Available from: https://doi.org/10.1890/04-1956

Bates, D., Mächler, M., Bolker, B.M. & Walker, S.C. (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1), 1–48. Available from: https://doi.org/10.18637/jss.v067.i01

Bosela, M., Popa, I., Gömöry, D., Longauer, R., Tobin, B., Kyncl, J. et al. (2016) Effects of post-glacial phylogeny and genetic diversity on the growth variability and climate sensitivity of European silver fir. *Journal of Ecology*, 104(3), 716–724. Available from: https://doi.org/10.1111/1365-2745.12561

Buckland, S.T., Burnham, K.P. & Augustin, N.H. (1997) Model selection: an integral part of inference. *Biometrics*, 603–618.

Cadotte, M.W., Cavender-Bares, J., Tilman, D. & Oakley, T.H. (2009) Using phylogenetic, functional and trait diversity to understand patterns of plant community productivity. *PLoS One*, 4(5), 1–9. Available from: https://doi.org/10.1371/journal.pone.0005695

Calcagno, V. & de Mazancourt, C. (2010) Glmulti: an R package for easy automated model selection with (generalized) linear models. *Journal of Statistical Software*, 34(12), 1–29. Available from: https://doi.org/10.18637/jss.v034.i12

Carpenter, B., Gelman, A., Hoffman, M.D., Lee, D., Goodrich, B., Betancourt, M. et al. (2017) Stan: a probabilistic programming language. *Journal of Statistical Software*, 76(1), 1–32. Available from: https://doi.org/10.18637/jss.v076.i01

Che-Castaldo, J., Che-Castaldo, C. & Neel, M.C. (2018) Predictability of demographic rates based on phylogeny and biological similarity. *Conservation Biology*, 32(6), 1290–1300. Available from: https://doi.org/10.1111/cobi.13135

Chesson, P. (2000) Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, 31(1), 343–366. Available from: https://doi.org/10.1146/annurev.ecolsys.31.1.343

Clark, J.S. (2010) Individuals and the variation needed for high species diversity in forest trees. *Science*, 327(5969), 1129–1132. Available from: https://doi.org/10.1126/science.1183506

Clark, J., Clark, A., Courbaud, B. et al. (2022) A universal coexistence hypothesis resolves the biodiversity paradox: species differences that generate diverse forests. *Authorea*. Available from: https://doi.org/10.22541/au.166029509.96486640/v1

Coelho de Souza, F., Dexter, K.G., Phillips, O.L., Brienen, R.J., Chave, J., Galbraith, D.R. et al. (2016) Evolutionary heritage influences Amazon tree ecology. *Proceedings of the Royal Society B: Biological Sciences*, 283(1844), 20161587. Available from: https://doi.org/10.1098/rspb.2016.1587

Comas, L.H., Bouma, T.J. & Eissenstat, D.M. (2002) Linking root traits to potential growth rate in six temperate tree species. *Oecologia*, 132(1), 34–43. Available from: https://doi.org/10.1007/s00442-002-0922-8

Comas, L.H. & Eissenstat, D. (2004) Linking fine root traits to maximum potential growth rate among 11 mature temperate tree species. *Functional Ecology*, 18, 388–397.

Conrad, O., Bechtel, B., Bock, M., Dietrich, H., Fischer, E., Gerlitz, L. et al. (2015) System for automated geoscientific analyses (SAGA) v. 2.1.4. *Geoscientific Model Development*, 8(7), 1991–2007. Available from: https://doi.org/10.5194/gmd-8-1991-2015

Craven, D., Hall, J.S., Berlyn, G.P., Ashton, M.S. & van Breugel, M. (2015) Changing gears during succession: shifting functional strategies in young tropical secondary forests. *Oecologia*, 179(1), 293–305. Available from: https://doi.org/10.1007/s00442-015-3339-x

Dalling, J.W., Swaine, M.D. & Garwood, N.C. (1998) Dispersal patterns and seed bank dynamics of pioneer trees in moist tropical forest. *Ecology*, 79(2), 564–578. Available from: https://doi.org/10.1890/0012-9658(1998)079[0564:DPASBD]2.0.CO;2

de Aguiar-Campos, N., Coelho de Souza, F., Maia, V.A., Rezende, V.L., de Souza, C.R., de Paula, G.G.P. et al. (2021) Evolutionary constraints on tree size and above-ground biomass in tropical dry forests. *Journal of Ecology*, 109(4), 1690–1702. Available from: https://doi.org/10.1111/1365-2745.13589

dos Santos, V.A.H.F. & Ferreira, M.J. (2020) Are photosynthetic leaf traits related to the first-year growth of tropical tree seedlings? A light-induced plasticity test in a secondary forest enrichment planting. *Forest Ecology and Management*, 460, 117900. Available from: https://doi.org/10.1016/j.foreco.2020.117900

Engelbrecht, B.M.J., Comita, L.S., Condit, R., Kursar, T.A., Tyree, M.T., Turner, B.L. et al. (2007) Drought sensitivity shapes species distribution patterns in tropical forests. *Nature*, 447(7140), 80–82. Available from: https://doi.org/10.1038/nature05747

Ferry, B., Morneau, F., Bontemps, J.-D., Blanc, L. & Freycon, V. (2010) Higher treefall rates on slopes and waterlogged soils result in lower stand biomass and productivity in a tropical rain forest. *Journal of Ecology*, 98(1), 106–116. Available from: https://doi.org/10.1111/j.1365-2745.2009.01604.x

Fine, P.V.A., Zapata, F. & Daly, D.C. (2014) Investigating processes of neotropical rain forest tree diversification by examining the evolution and historical biogeography of the protieae (Burseraceae). *Evolution*, 68(7), 1988–2004. Available from: https://doi.org/10.1111/evo.12414

Fortunel, C., Lasky, J.R., Uriarte, M., Valencia, R., Wright, S.J., Garwood, N.C. et al. (2018) Topography and neighborhood crowding can interact to shape species growth and distribution in a diverse Amazonian forest. *Ecology*, 99, 2272–2283. Available from: https://doi.org/10.1002/ecy.2441

Gourlet-Fleury, S., Guehl, J.-M. & Laroussine, O. (2004) *Ecology and management of a neotropical rainforest: lessons drawn from Paracou, a long-term experimental research site in French Guiana ecology and management of a neotropical rainforest: lessons drawn from Paracou, a long-term experimental research sit*. Paris: Elsevier. Retrieved from http://agritrop.cirad.fr/522004/

Grattapaglia, D., Plomion, C., Kirst, M. & Sederoff, R.R. (2009) Genomics of growth traits in forest trees. *Current Opinion in Plant Biology*. Elsevier Current Trends., 12, 148–156. Available from: https://doi.org/10.1016/j.pbi.2008.12.008

Greenwell, B., Boehmke, B., Cunningham, J. & GBM Developers. (2022) gbm: Generalized Boosted Regression Models. R package version 2.1.8.1. https://CRAN.R-project.org/package=gbm

Grömping, U. (2006) Relative importance for linear regression in R: the package relaimpo. *Journal of Statistical Software*, 17(1), 1–27. Available from: https://doi.org/10.18637/jss.v017.i01

Hérault, B., Bachelot, B., Poorter, L., Rossi, V., Bongers, F., Chave, J. et al. (2011) Functional traits shape ontogenetic growth trajectories of rain forest tree species: plant traits shape growth

trajectory. *Journal of Ecology*, 99(6), 1431–1440. Available from: https://doi.org/10.1111/j.1365-2745.2011.01883.x

Herault, B., Ouallet, J., Blanc, L., Wagner, F. & Baraloto, C. (2010) Growth responses of neotropical trees to logging gaps. *Journal of Applied Ecology*, 47(4), 821–831. Available from: https://doi.org/10.1111/j.1365-2664.2010.01826.x

Hérault, B. & Piponiot, C. (2018) Key drivers of ecosystem recovery after disturbance in a neotropical forest. *Forest Ecosystems*, 5(1), 2. Available from: https://doi.org/10.1186/s40663-017-0126-7

Jin, Y. & Qian, H. (2019) V. PhyloMaker: an R package that can generate very large phylogenies for vascular plants. *Ecography*, 42(8), 1353–1359. Available from: https://doi.org/10.1111/ecog.04434

John, R., Dalling, J.W., Harms, K.E., Yavitt, J.B., Stallard, R.F., Mirabello, M. et al. (2007) Soil nutrients influence spatial distributions of tropical tree species. *Proceedings of the National Academy of Sciences of the United States of America*, 104(3), 864–869. Available from: https://doi.org/10.1073/pnas.0604666104

Keck, F., Rimet, F., Bouchez, A. & Franc, A. (2016) Phylosignal: an R package to measure, test, and explore the phylogenetic signal. *Ecology and Evolution*, 6(9), 2774–2780. Available from: https://doi.org/10.1002/ece3.2051

King, D.A., Davies, S.J., Nur Supardi, M.N. & Tan, S. (2005) Tree growth is related to light interception and wood density in two mixed dipterocarp forests of Malaysia. *Functional Ecology*, 19(3), 445–453. Available from: https://doi.org/10.1111/j.1365-2435.2005.00982.x

King, D.A., Davies, S.J., Tan, S. & Noor, N.S.M. (2006) The role of wood density and stem support costs in the growth and mortality of tropical trees. *Journal of Ecology*, 94(3), 670–680. https://doi.org/10.1111/j.1365-2745.2006.01112.x.

Körner, C. (2017) A matter of tree longevity. *Science*, 355(6321), 130–131. Available from: https://doi.org/10.1126/science.aal2449

Le Bec, J., Courbaud, B., Moguédec, G.L. & Pélissier, R. (2015) Characterizing tropical tree species growth strategies: learning from inter-individual variability and scale invariance. *PLoS One*, 10(3), e0117028. Available from: https://doi.org/10.1371/journal.pone.0117028

Lewis, S.L. & Tanner, E.V.J. (2000) Effects of above- and below-ground competition on growth and survival of rain forest tree seedlings. *Ecology*, 81(9), 2525–2538. Available from: https://doi.org/10.1890/0012-9658(2000)081[2525:EOAABC]2.0.CO;2

Lichstein, J.W., Dushoff, J., Levin, S.A. & Pacala, S.W. (2007) Intraspecific variation and species coexistence. *The American Naturalist*, 170(6), 807–818. Available from: https://doi.org/10.1086/522937

Lindeman, R. H., Merenda, P. F., & Gold, R. Z. (1980). *Introduction to bivariate and multivariate analysis*. Glenview, Ill: Scott, Foresman.

Ma, Z., Guo, D., Xu, X., Lu, M., Bardgett, R.D., Eissenstat, D.M. et al. (2018) Evolutionary history resolves global organization of root functional traits. *Nature*, 555(7694), 94–97. Available from: https://doi.org/10.1038/nature25783

Martinez-Ramos, M., Alvarez-Buylla, E. & Sarukhan, J. (1989) Tree demography and gap dynamics in a tropical RainForest. *Ecology*, 70(3), 555–558. Available from: https://doi.org/10.2307/1940203

Molino, J.-F. & Sabatier, D. (2001) Tree diversity in tropical rain forests: a validation of the intermediate disturbance hypothesis. *Science*, 294(5547), 1702–1704. Available from: https://doi.org/10.1126/science.1060284

Nakagawa, S. & Schielzeth, H. (2013) A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, 4(2), 133–142. Available from: https://doi.org/10.1111/j.2041-210x.2012.00261.x

O'Brien, M.J. & Escudero, A. (2021) Topography in tropical forests enhances growth and survival differences within and among species via water availability and biotic interactions.

Functional Ecology, 1–13, 686–698. Available from: https://doi.org/10.1111/1365-2435.13977

Osazuwa-Peters, O.L., Wright, S.J. & Zanne, A.E. (2017) Linking wood traits to vital rates in tropical rainforest trees: insights from comparing sapling and adult wood. *American Journal of Botany*, 104(10), 1464–1473. Available from: https://doi.org/10.3732/ajb.1700242

Peña-Claros, M., Fredericksen, T.S., Alarcón, A., Blate, G.M., Choque, U., Leaño, C. et al. (2008) Beyond reduced-impact logging: silvicultural treatments to increase growth rates of tropical trees. *Forest Ecology and Management*, 256(7), 1458–1467. Available from: https://doi.org/10.1016/j.foreco.2007.11.013

Philipson, C.D., Dent, D.H., O'Brien, M.J., Chamagne, J., Dzulkifli, D., Nilus, R. et al. (2014) A trait-based trade-off between growth and mortality: evidence from 15 tropical tree species using size-specific relative growth rates. *Ecology and Evolution*, 4(18), 3675–3688. Available from: https://doi.org/10.1002/ece3.1186

Poorter, L., Castilho, C.V., Schietti, J., Oliveira, R.S. & Costa, F.R.C. (2018) Can traits predict individual growth performance? A test in a hyperdiverse tropical forest. *New Phytologist*, 219(1), 109–121. Available from: https://doi.org/10.1111/nph.15206

Poorter, L., McDonald, I., Alarcón, A., Fichtler, E., Licona, J.C., Peña-Claros, M. et al. (2010) The importance of wood traits and hydraulic conductance for the performance and life history strategies of 42 rainforest tree species. *New Phytologist*, 185(2), 481–492. Available from: https://doi.org/10.1111/j.1469-8137.2009.03092.x

Potvin, C. & Gotelli, N.J. (2008) Biodiversity enhances individual performance but does not affect survivorship in tropical trees. *Ecology Letters*, 11(3), 217–223. Available from: https://doi.org/10.1111/j.1461-0248.2007.01148.x

R Core Team. (2020) *R: a language and environment for statistical computing*. Vienna, Austria. https://www.R-project.org/

Reich, P.B. (2014) The world-wide "fast–slow" plant economics spectrum: a traits manifesto. *Journal of Ecology*, 102(2), 275–301. Available from: https://doi.org/10.1111/1365-2745.12211

Rüger, N., Berger, U., Hubbell, S.P., Vieilledent, G. & Condit, R. (2011) Growth strategies of tropical tree species: disentangling light and size effects. *PLoS One*, 6(9), e25330. Available from: https://doi.org/10.1371/journal.pone.0025330

Rüger, N., Condit, R., Dent, D.H., DeWalt, S.J., Hubbell, S.P., Lichstein, J.W. et al. (2020) Demographic trade-offs predict tropical forest dynamics. *Science*, 368(6487), 165–168. Available from: https://doi.org/10.1126/science.aaz4797

Russo, S.E., Brown, P., Tan, S. & Davies, S.J. (2008) Interspecific demographic trade-offs and soil-related habitat associations of tree species along resource gradients. *Journal of Ecology*, 96(1), 192–203. Available from: https://doi.org/10.1111/j.1365-2745.2007.01330.x

Schmitt, S., Hérault, B., Ducouret, É., Baranger, A., Tysklind, N., Heuertz, M. et al. (2020) Topography consistently drives intra- and inter-specific leaf trait variation within tree species complexes in a neotropical forest. *Oikos*, 129(10), 1521–1530. Available from: https://doi.org/10.1111/oik.07488

Schmitt, S., Maréchaux, I., Chave, J., Fischer, F.J., Piponiot, C., Traissac, S. et al. (2020) Functional diversity improves tropical forest resilience: insights from a long-term virtual experiment. *Journal of Ecology*, 108(3), 831–843. Available from: https://doi.org/10.1111/1365-2745.13320

Schmitt, S., Tysklind, N., Derroire, G., Heuertz, M. & Hérault, B. (2021) Topography shapes the local coexistence of tree species within species complexes of neotropical forests. *Oecologia*, 196(2), 389–398. Available from: https://doi.org/10.1007/s00442-021-04939-2

Schmitt, S., Tysklind, N., Hérault, B. & Heuertz, M. (2021) Topography drives microgeographic adaptations of closely related species in two tropical tree species complexes. *Molecular Ecology*, 30(20), 5080–5093. Available from: https://doi.org/10.1111/mec.16116

Schmitt, S., Tysklind, N., Heuertz, M. & Hérault, B. (2022) Selection in space and time: individual tree growth is adapted to tropical

forest gap dynamics. *Molecular Ecology*. Available from: https://doi.org/10.1111/mec.16392

Smith, S.A. & Brown, J.W. (2018) Constructing a broadly inclusive seed plant phylogeny. *American Journal of Botany*, 105(3), 302–314. Available from: https://doi.org/10.1002/ajb2.1019

Stan Development Team. (2018) Rstan: the R interface to Stan. Retrieved from http://mc-stan.org/

Stump, S.M., Song, C., Saavedra, S., Levine, J.M. & Vasseur, D.A. (2022) Synthesizing the effects of individual-level variation on coexistence. *Ecological Monographs*, 92(1), e01493. Available from: https://doi.org/10.1002/ECM.1493

Svenning, J.C., Eiserhardt, W.L., Normand, S., Ordonez, A. & Sandel, B. (2015) The influence of paleoclimate on present-day patterns in biodiversity and ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, 46, 551–572. Available from: https://doi.org/10.1146/annurev-ecolsys-112414-054314

Swenson, N.G. (2013) The assembly of tropical tree communities—the advances and shortcomings of phylogenetic and functional trait analyses. *Ecography*, 36(3), 264–276. Available from: https://doi.org/10.1111/j.1600-0587.2012.00121.x

Uriarte, M., Canham, C.D., Thompson, J. & Zimmerman, J.K. (2004) A neighborhood analysis of tree growth and survival in a hurricane-driven tropical forest. *Ecological Monographs*, 74(4), 591–614. Available from: https://doi.org/10.1890/03-4031

Uriarte, M., Condit, R., Canham, C.D. & Hubbell, S.P. (2004) A spatially explicit model of sapling growth in a tropical forest: does the identity of neighbours matter? *Journal of Ecology*, 92(2), 348–360. Available from: https://doi.org/10.1111/j.0022-0477.2004.00867.x

Vehtari, A., Gelman, A. & Gabry, J. (2017) Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Statistics and Computing*, 27(5), 1413–1432. Available from: https://doi.org/10.1007/s11222-016-9696-4

Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. et al. (2007) Let the concept of trait be functional! *Oikos*, 116(5), 882–892. Available from: https://doi.org/10.1111/j.0030-1299.2007.15559.x

Visser, M.D., Bruijning, M., Wright, S.J., Muller-Landau, H.C., Jongejans, E., Comita, L.S. et al. (2016) Functional traits as predictors of vital rates across the life cycle of tropical trees. *Functional Ecology*, 30(2), 168–180. Available from: https://doi.org/10.1111/1365-2435.12621

Vleminckx, J., Fortunel, C., Valverde-Barrantes, O., Timothy Paine, C.E., Engel, J., Petronelli, P. et al. (2021) Resolving whole-plant economics from leaf, stem and root traits of 1467 Amazonian tree species. *Oikos*, 130(7), 1193–1208. Available from: https://doi.org/10.1111/oik.08284

Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L., François, R. et al. (2019) Welcome to the Tidyverse. *Journal of Open Source Software*, 4(43), 1686. Available from: https://doi.org/10.21105/joss.01686

Wright, S.J., Kitajima, K., Kraft, N.J.B., Reich, P.B., Wright, I.J., Bunker, D.E. et al. (2010) Functional traits and the growth-mortality trade-off in tropical trees. *Ecology*, 91(12), 3664–3674. Available from: https://doi.org/10.1890/09-2335.1

Xiang, W., Wu, W., Tong, J., Deng, X., Tian, D., Zhang, L. et al. (2013) Differences in fine root traits between early and late-successional tree species in a Chinese subtropical forest. *Forestry*, 86(3), 343–351. Available from: https://doi.org/10.1093/forestry/cpt003

Yang, J., Cao, M. & Swenson, N.G. (2018) Why functional traits do not predict tree demographic rates. *Trends in Ecology and Evolution*, 33(5), 326–336. Available from: https://doi.org/10.1016/j.tree.2018.03.003

Yu, G. (2020) Using ggtree to visualize data on tree-like structures. *Current Protocols in Bioinformatics*, 69(1), 1–18. Available from: https://doi.org/10.1002/cpbi.96

Zanne, A.E., Tank, D.C., Cornwell, W.K., Eastman, J.M., Smith, S.A., FitzJohn, R.G. et al. (2014) Three keys to the radiation of angiosperms into freezing environments. *Nature*, 506(7486), 89–92. Available from: https://doi.org/10.1038/nature12872

SUPPORTING INFORMATION

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

How to cite this article: Schmitt, S., Hérault, B. & Derroire, G. (2023) High intraspecific growth variability despite strong evolutionary legacy in an Amazonian forest. *Ecology Letters*, 26, 2135–2146. Available from: https://doi.org/10.1111/ele.14318