

Summary

Introduction

Functional ecology aims to understand ecology with a different approach from the historical phylogenetic perspective, instead through the core concept of functional trait to unravel the different functions at different scales (McGill et al., 2006). Functional traits are measurable properties of organisms that strongly influence organismal performance (McGill et al., 2006), relating indirectly to the fitness of an individual. Performance can be defined as a measurable quantity enabling comparison between species on their capacity to maintain biomass over generations.

In Functional Ecology, numerous papers underline the importance of taking intra-specific variability into account (Violle and Jiang, 2009; Albert et al., 2011). Intra-specific variability is the variability existing between individuals of the same species, compared to inter-specific variability which is the variability between different sets of species. Growth model developed by Hérault et al. (2011) for example consider only inter-specific variability, the model assume that all individuals of a given species share the same traits: the average traits of all individuals of the species. Several studies reviewed by Violle et al. (2012) underline the importance of intra-specific variability for our understanding of species coexistence for example; a tree with traits different from its species average may occupy a slightly different ecological niche and thus coexist in some cases, while models considering only inter-specific variability would not predict such coexistence (Clark et al., 2010; Paine et al., 2011).

As underlined above, intra-specific variability holds some information about the specific niche occupied by an individual, however, growth models still do not include it and consider all trees as behaving the same. Thus we wondered (i) how intra-specific variabilities was structured both in traits and in performance compared to inter-specific variabilities, (ii) what the origin of those intra-specific variabilities were, (iii) if they were related, i.e. does a tree with traits very different from its species average has a growth very different from its species average, (iv) does intra-specific variability in traits needs to be taken into account in growth models, (v) are there specific patterns of performance taking each trait separately looking at individual's position from species average trait.

In the context Amazonian forest, which is a Neotropical forest, performance indexes may be complex to measures. Widely used indexes include tree height, seed number, flower number or tree diameter, because of vegetation density tree diameter is the only reliable measurement. We focused here on 9 1-ha plots spread over French Guiana along precipitation and geological gradient, where 16 traits were measured (Baraloto et al., 2010), and tree diameter was followed for several decades, comprising a total of 3483 trees. Because all measured trees were botanically determined, we can study the inter-specific as well as the intra-specific variability both in performance and in traits.

Materials and Methods

Data Provenance

Growth Data

The first data set is an inventory of all trees over 10cm in Diameter at Breast Height (DBH), i.e. measured at 1.3m high, in nine 1-ha plots in French Guiana (see map [\[missing figure\]](#)). In each plot, trees diameter were measured every two or five years depending on the plot.

We selected a common measured period between 2001 and 2013 comprising a total of 3549 trees; we estimated annual growth rate (AGR) in diameter by fitting a linear regression of DBH over years. The slope of the regression gave us an average AGR for each followed tree on the comprised

Trait Data

The second data set comes was a collection of five functional traits (see [Table 1](#)) extracted from a bigger database ([Baraloto et al., 2010](#)) on the same trees. Traits were not followed through time and measured only once. Selected traits are related to leaf and wood economics spectrum([Westoby, 1998](#); [Baraloto et al., 2010](#)).

Leaf economics spectrum. Specific Leaf Area (SLA) is the photo-sensitive area per unit of dry mass of the leaf; high SLA underlines investment on high light-capturing leaves that have a short pay-back time per gram of dry matter invested; while low SLA reflects strategies with less light-capturing leaves and longer payback time that may appear competitive in some conditions. Total leaf chlorophyll content reflects the global strategy of the plant of having resource-expansive leaves with high payback or resource-cheap leaves with lower payback. Laminar toughness measures the resistance of a leaf to pinching, high toughness values correlates with low herbivory rate, it correlates with defense strategy ([Westoby, 1998](#)).

Stem economics spectrum. Wood density underlines different ecological strategy for trees, a low wood density makes wood less stable and less better protected against herbivory but cheap volumetric construction cost because of low resource requirements; while a high wood density makes the tree more stable but with higher construction cost, meaning a lower growth. Trunk bark thickness associate with defense strategies in neotropical forests, thicker bark provides higher resistance to pathogens and herbivores ([Paine et al., 2010](#)).

Analysis of Variance

Variance partitioning was done using a one-way Analysis of Variance, we explained either individual traits by a species effect and an individual term error, as follows:

$$\text{Tr}_{i,s} = \mu_s + \epsilon_i, \quad (1)$$

with $\text{Tr}_{i,s}$, the trait of individual i of species s ; μ_s the mean trait of species s ; ϵ_i the individual error term with a Gaussian distribution. The explained variance by the species effect can then be expressed by the proportion of group sum of squares over the total sum of squares. We considered the residual sum of squares as being the individual variance. We partitioned the variance similarly for AGR.

Growth model

To predict the growth of tree from a single trait we used a linear mixed-model with the general formula:

$$\log(\text{AGR}_{i,s,p} + 1) = \theta_0 + \gamma_{0,s} + \gamma_p + (\theta_1 + \gamma_{1,s}) \times \text{DBH} + (\theta_2 + \gamma_{2,s}) \times \log(\text{DBH}) + \delta + \epsilon_i, \quad (2)$$

Trait Name	Units	Role	Best Growth models
Trunk bark thickness	mm	Stem economics	Absolute Distance
Xylem density (wood density)	g.cm ⁻³	Stem economics	Individual Distance*
Specific Leaf Area (SLA)	cm ² .g ⁻¹	Leaf economics	Individual Distance
Laminar total chlorophyll	µm.mm ⁻²	Leaf economics	Individual Distance*
Laminar toughness	N	Leaf economics	Individual Distance*

Table 1: Selected functional traits. Stem and Leaf Economics Spectrum are defined as in (Baraloto et al., 2010), the two axes unravel distinct ecological strategies (see Materials and Methods for more details). The "Best Growth Model" column shows which growth model (Equation 2) explained best individual trait values. *: Individual and Absolute distances models had similar performances.

with $\epsilon_i \sim \mathcal{N}(0, \theta_3)$ the individual residual, where $\text{AGR}_{i,s,p}$ is the AGR of tree i of species s in plot p ; $\theta_0 \dots \theta_3$ are parameters to be estimated; $\gamma_{0,s} \dots \gamma_{2,s}$ and γ_p follow a centered Gaussian distribution with unknown variances $\sigma_{0,s}^2 \dots \sigma_{2,s}^2$ and σ_p^2 . Tr_s is the average trait value for species s .

To understand how the distance to species average value affected the predicted growth, we used different δ values:

$$\delta = \begin{cases} \theta_4 \times \text{Tr}_s \\ \theta_4 \times \text{Tr}_s + \theta_5 \times (\text{Tr}_i - \text{Tr}_s) \\ \theta_4 \times \text{Tr}_s + \theta'_5 \times |\text{Tr}_i - \text{Tr}_s| \\ \theta'_4 \times \text{Tr}_i \end{cases} \quad (3)$$

Tr_s the species average value, with a parameter θ_4 ; $\text{Tr}_i - \text{Tr}_s$ the distance of individual trait value Tr_i to species average, with the species term Tr_s ; or $|\text{Tr}_i - \text{Tr}_s|$ the absolute distance to species average trait, with the species term Tr_s ; or Tr_i the individual trait value.

Our models tested the difference of prediction between using only the species average trait value to predict growth and the same term plus an individual distance term (real or absolute) vs. the individual trait value.

Simulations

For each trait, we selected the best growth model with both the highest adapted R-squared for mixed models (Nakagawa and Schielzeth, 2013) and lowest Akaike Information Criterion (AIC); between models with either individual distance to species trait average or the absolute value of this distance (see Table 1). We simulated regularly spaced values of both the species average trait value and the distance to species average, within the 5th and 95th centiles of our data. From those simulated values, with fixed DBH value, we used growth models to predict AGR, depending on both species average and distance to species average trait value.

Data analysis

All data analyses were made using R (R Core Team, 2015) version 3.2.0 (2015-04-16), plots were made with ggplot2 (Wickham, 2009). We fit mixed-models with lme4 R package (Bates et al., 2014) 1.1-7 and computed adapted R-squared for mixed-models (Nakagawa and Schielzeth, 2013) implemented in MuMIn R package (Bartón, 2015) version 1.13.4.

Results

Using a one-way ANOVA, we partitioned variance due to the species effect, i.e. the part of the variance explained by the species of individuals (see [Figure 1](#)). Depending on the trait, the species effect could explain between 27% up to 75% of the variability of our data. While species effect can explain over 75% of the variability in wood density, it only explains less than 30% of the variability in AGR. The specific effect is strong for certain traits (wood density, toughness and SLA), but not for AGR.

Several other factors may explain residual variability: micro-environmental conditions, intra-specific variability or climatic conditions for example. In order to disentangle better the residual variance, we tested spatial auto-correlation of traits and AGR on our plots with mark correlation functions (data not shown). Neither traits nor AGR were spatially auto-correlated, i.e. the distribution of AGR or trait values in our 9 plots is not specifically distributed, indeed it is not very different from random distribution of those values in the plots. It underlines that in our data set the micro-environment does not strongly influence the traits.

From a functional point of view, the growth of individual may be explained by its traits. To test this assumption we made growth mixed-model including all selected traits of our data set (see [Table 1](#)) as predictors of the AGR, with both a species and a plot random effect. From previous growth model **[citation needed]** we knew diameter at breast height (DBH) as well as $\log(\text{DBH})$ improve AGR predictions and thus we added those two terms in our models.

An individual's trait is its species average trait plus its difference to this average. For some traits, considering the absolute distance to average trait may model better actual processes, as the important factor, in performance, is the absolute distance to species average trait. To understand whether we have to consider intra-specific variability in our data set, we compared models with individual trait value vs. models with specific trait value to which we added individual's distance measures (real or absolute); all those models were compared to the ones with only the specific trait value. We both computed models including all traits, or trait-specific models. In the end, our models predict AGR with DBH and $\log(\text{DBH})$ factors, plus species random effect both on intercept and slopes of these two factors, we added a plot intercept random effect as it improved much the R-squared of our models, and then different trait terms. **[missing figure]**table of characteristics of models?)

The best model was the individual ones in term of R-squared. However, the model with real individual distance predicted AGR better than the one with only specific term.

We then examined the link between predicted AGR and distance to species average for each trait separately. We computed regularly spaced species average trait values in the 5%-95% of species average trait values in our data set as well as individual's distance to species average in the same 5%-95% range of values in our data set. We then associated every individual's distance to every species average trait, giving us all possible couples. From this grid of data, we predicted AGR of those simulated individuals using previous trait-specific model, using the data median DBH value. For each trait we selected the model with the highest R-squared with the lowest AIC (see [Table 1](#)'s last column). The best model for bark thickness had an absolute distance to species average trait term, while for all the other traits the best models were those with real (with sign) distance to species average trait.

For each trait we had AGR predictions from models for a given range of data ([Figure 2](#)), unraveling patterns of change in AGR with individual's distance or with species average trait. For example, AGR increases with decreasing individual's distance in SLA.

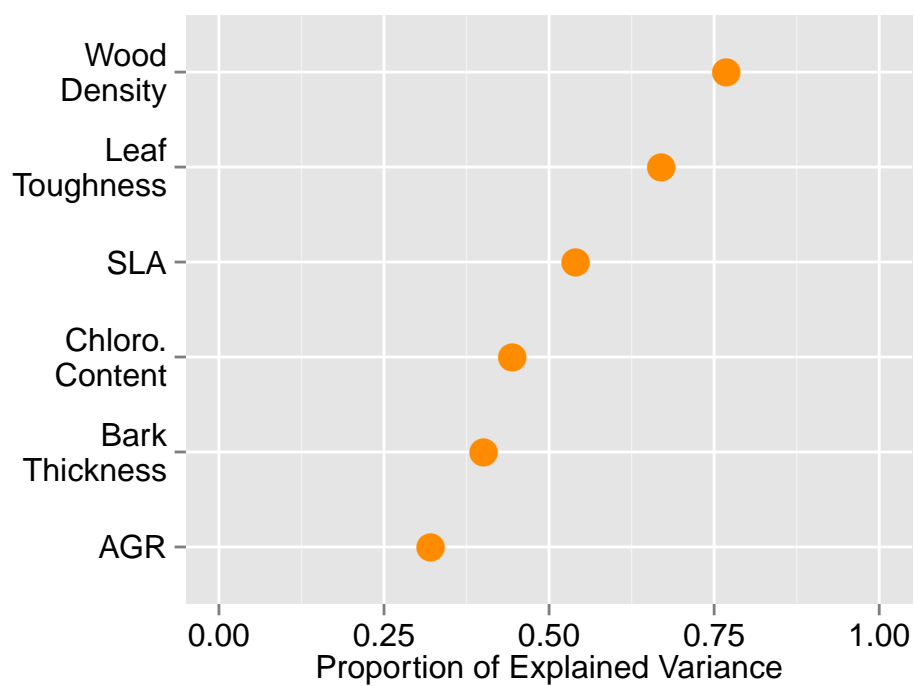


Figure 1: Explained variance by species effect in ANOVAs. Dot-plot of explained variance in ANOVA by the species effect for traits and AGR. The right space after the orange is the residual variance. **Chloro. Content:** Laminar Chlorophyll Content, **AGR:** Annual Growth Rate (in diameter).

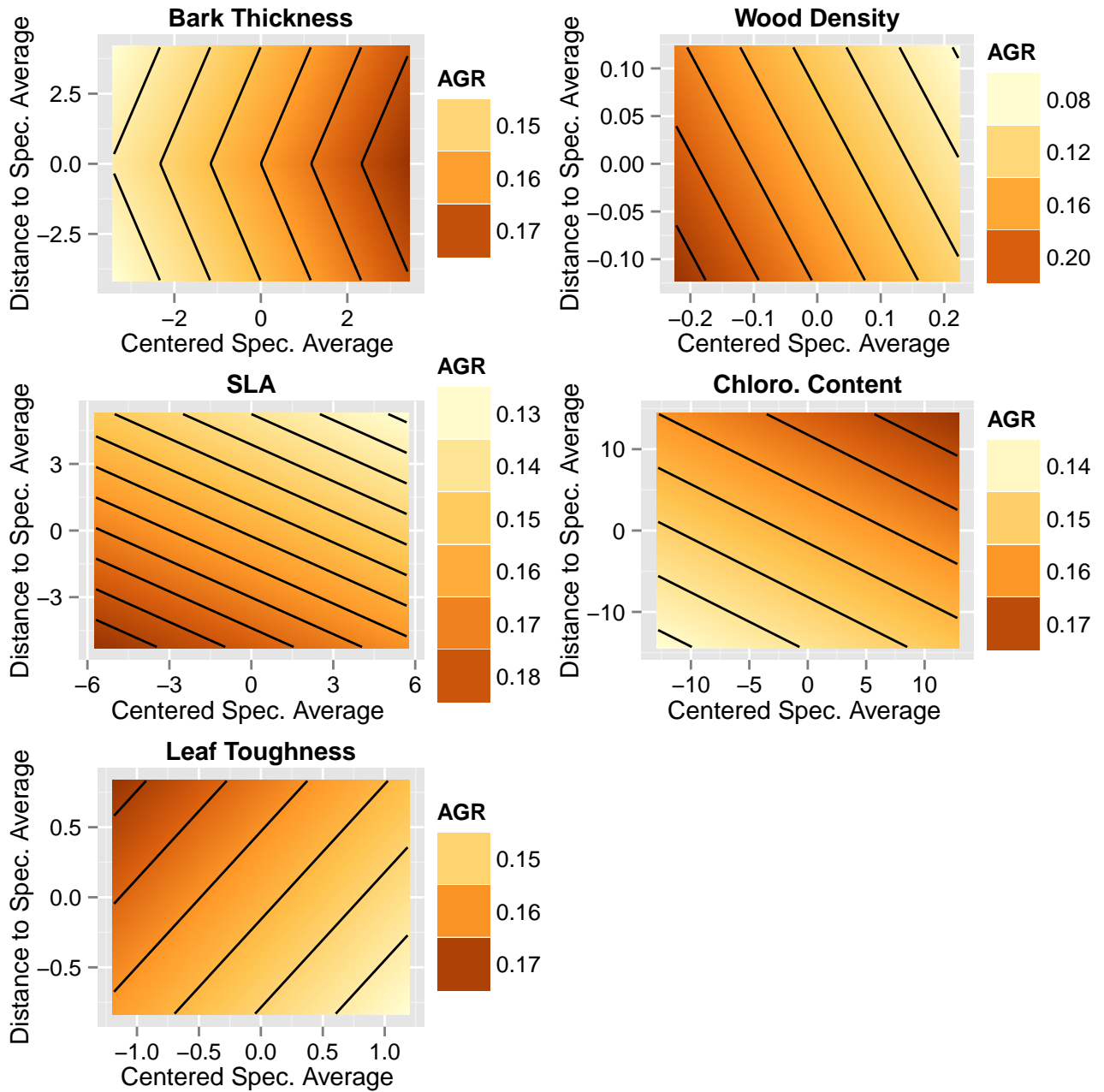


Figure 2: Simulations of species trait and predictions of AGR with growth models. Surface plots of predicted AGR of simulated range of data: X-axis, centered species average trait (species average trait minus mean of all species average trait); Y-axis, individual distance to species average trait. Black lines are equal-AGR lines over the surface, i.e. on those line each point has the same AGR value. For details on traits see [Table 1](#).

Discussion

From our data set we showed that taking into account intra-specific variability does not improve much growth models; compared to the extensive sampling needed to measure individual traits. Using simulations, we also showed how individual's trait had implications of tree performance when compared to its species average trait.

Taking intra-specific variability into account has been a running debate in functional ecology, it is a trade-off between the cost of sampling several individuals per species and the information gained by such sampling (Albert et al., 2011; Violle et al., 2012). Indeed, in our data set, for growth in diameter, it seemed reasonable to link intra-specific growth variability to traits intra-specific variabilities; however, we have shown here that those variabilities are not related. Thus, in our case, averaging traits for entire species, and consider each individual as an average of all other individuals in its species does not affect predictive performances.

It still raises the question of what causes those two independent variabilities. We failed to reveal a micro-environmental effect by studying spatial auto-correlation in both traits and AGR, whereas traits variation along spatial gradient has been shown in some cases [citation needed]. Here we did not look at the influence of neighboring trees on a focal tree traits, it may drive intra-specific trait variability. The niche differentiation hypothesis for example drive trees towards trait values that distinct from their neighbors'.

We showed that depending on the trait, intra-specific variability may have various consequences on AGR patterns. An individual moving away from its species average bark thickness, has a lower AGR than an other individual of the same species, with the same average species value; individuals at the species average value have greater AGR. An increase in bark thickness average species value also increases performance, there is a trade-off between individual's distance and species average bark thickness values. We would imagine a species to increase its performance (=AGR) and thus increase its bark thickness average value, however, for this to happen certain individuals would have greater bark thickness than the species average value, decreasing their performance. If our performance index reflect the probable evolutionary landscape, we would then be in a situation of stable average species value. Whereas for wood density increasing the individual's distance decreases performance, and increasing species average wood density decreases AGR; from an evolutionary point of view, we would see a continuous decrease in wood density, maximizing AGR. However, we observe stable phenotypes for species [citation needed] on their trait, mainly because our performance index does not reflect the evolutionary landscape and fitness properly. AGR in diameter instead is a proxy of survival only, a bigger tree diameter has a higher survival rate than a smaller tree, AGR does not reflect reproduction nor seed survival. Performance indexes may be proxies of fitness, but they underline different ecological or evolutionary strategies, and care should be taken when interpreting performance landscapes.

Our simulations still unravel new trade-offs, between individual trait and its species average trait. Abundant studies showed trade-offs between traits [citation needed], but, to our knowledge, it is the first time that a trade-off, for the same trait, has been shown between intra-specific variability and species average value. Taking SLA for example, individual's distance and species average trait pull in opposite directions for AGR: increasing individual's SLA increases AGR, but increasing species average SLA decreases AGR. Those trade-offs

Authors Contributions and Acknowledgments

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