Summary

Introduction

Functional ecology aims to understand ecology not using the historical phylogenetic perspective, but 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.

From Hutchinson definition of *fundamental niche* (Hutchinson, 1957), Violle and Jiang (2009) extended the definition to become a *functional niche*—a multi-dimensional volume, also called the *functional space* ; it is an n-dimensional space defined by measures on n traits. In such a space an individual is defined by all the values of its traits, each one on a distinct axis. In three dimensions, the species niche would be the volume encompassing all its individuals; the center of gravity of the cloud would be the species average trait values, defining niche position, while the shape of the general "cloud" would define niche breadth, as suggested by Violle and Jiang (2009).

The concept of functional niche helps understand community ecology and assemblage. In this view, two species would coexist if their functional volumes would not intersect. The high number of dimensions, i.e. traits, of the functional "hyper-volume" as called by **[citation needed]** makes it difficult to apprehend: the volume may have "holes" where some trait combinations are impossible. An individual is located by its own trait values or relatively to its species average. The distance from species average translates the intra-specific variability in the species.

Species functional niche reflects their ecological strategies. For plants, four traits have been identified to underline distinct strategies: the classical Leaf Area - Height - Seed mass triangle, suggested by **[citation needed]**; as well as wood economics spectrum traits (Baraloto et al., 2010).

Functional trait $\rightarrow$ performance indexes $\rightarrow$ fitness, performance indexes reflect fitness, thus evolution. Linking functional traits and performance indexes $\rightarrow$ predict the evolution of functional traits. How then species position do not change over time to increase performance? Some case, such as wood density, where we would expect species to decrease it to have faster growth two answers: resource-energy trade-offs (darwinian demons) or specific strategy.

Those trade-offs are generally shown at the species level by comparing several species showing impossible trait combinations, i.e. in the previous example it would be impossible to find species with dense wood and fast growth. However, if we want to investigate not a general trade-off that exists at the species level, but how the position of an individual compared to the species average may influence performance indexes. For example, a tree with a less dense wood than its species average would have a higher growth rate than individuals with a density around the species average. Throughout this paper we try to understand how the performance of an individual is affected by the distance to its species average trait.

For certain traits, we would expect the species position not to vary, thus, our approach may unravel new trade-offs between intra-specific and inter-specific variablities.

Diameter Growth & Tropical Forests $\rightarrow$ French Guiana Context

Several growth models created, used $\rightarrow$ estimate growth using measured 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 payback 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.

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 **[citation needed]**.

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:

$$\mathrm{Tr}_{i,s} = \mu_s + \epsilon_i, \tag{1}$$

with $\mathrm{Tr}_{i,s}$, 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:

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

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	$\mu m.mm^{-2}$	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 distance and Absolute distance model with 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; $\theta_0 \ldots \theta_3$ are parameters to be estimated; $\gamma_{0,s} \ldots \gamma_{2,s}$ and γ_p follow a centered Gaussian distribution with unknown variances $\sigma^2_{0,s} \ldots \sigma^2_{2,s}$ and σ^2_p; 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: $\theta_4 \times \text{Tr}_s$ the species average value, with a parameter θ_4; $\theta_4 \times \text{Tr}_s + \theta_5 \times (\text{Tr}_i - \text{Tr}_s)$ the distance of individual trait value Tr_i to species average, with the species term Tr_s; or $\theta_4 \times \text{Tr}_s + \theta'_5 \times |\text{Tr}_i - \text{Tr}_s|$ the absolute distance to species average trait, with the species term Tr_s; or $\theta'_4 \times \text{Tr}_i$ 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 5^{th} and 95^{th} 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 (Bartoń, 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(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(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.

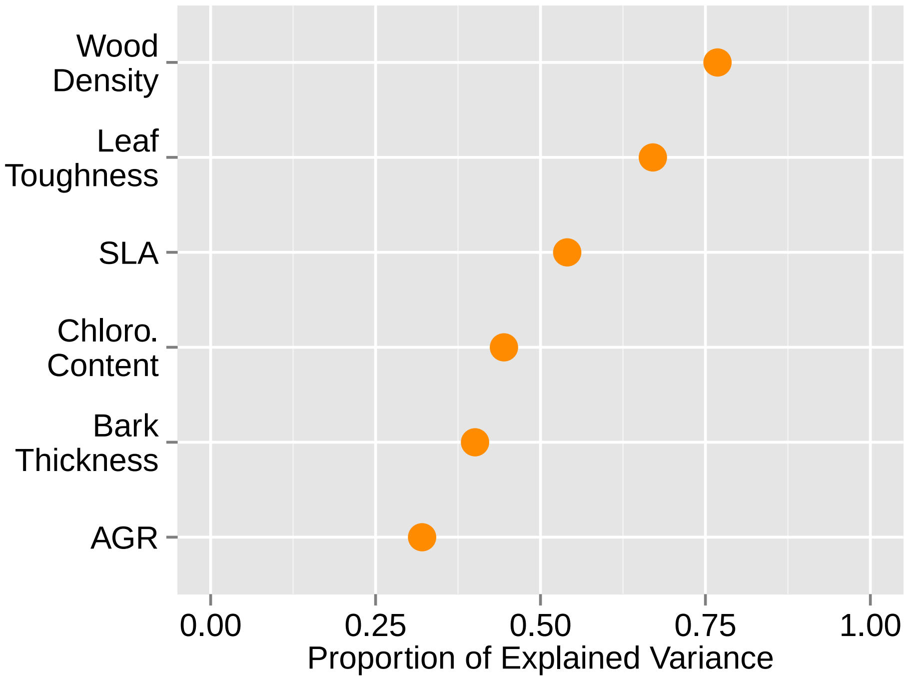

Figure 1: Explained variance by species effect in ANOVAs. Dot-plot of explained variance in ANOVA by the species effect for traits and AGR. The right space after the orange is the residual variance. **Chloro. Content**: Laminar Chlorophyll Content, **AGR**: Annual Growth Rate (in diameter).

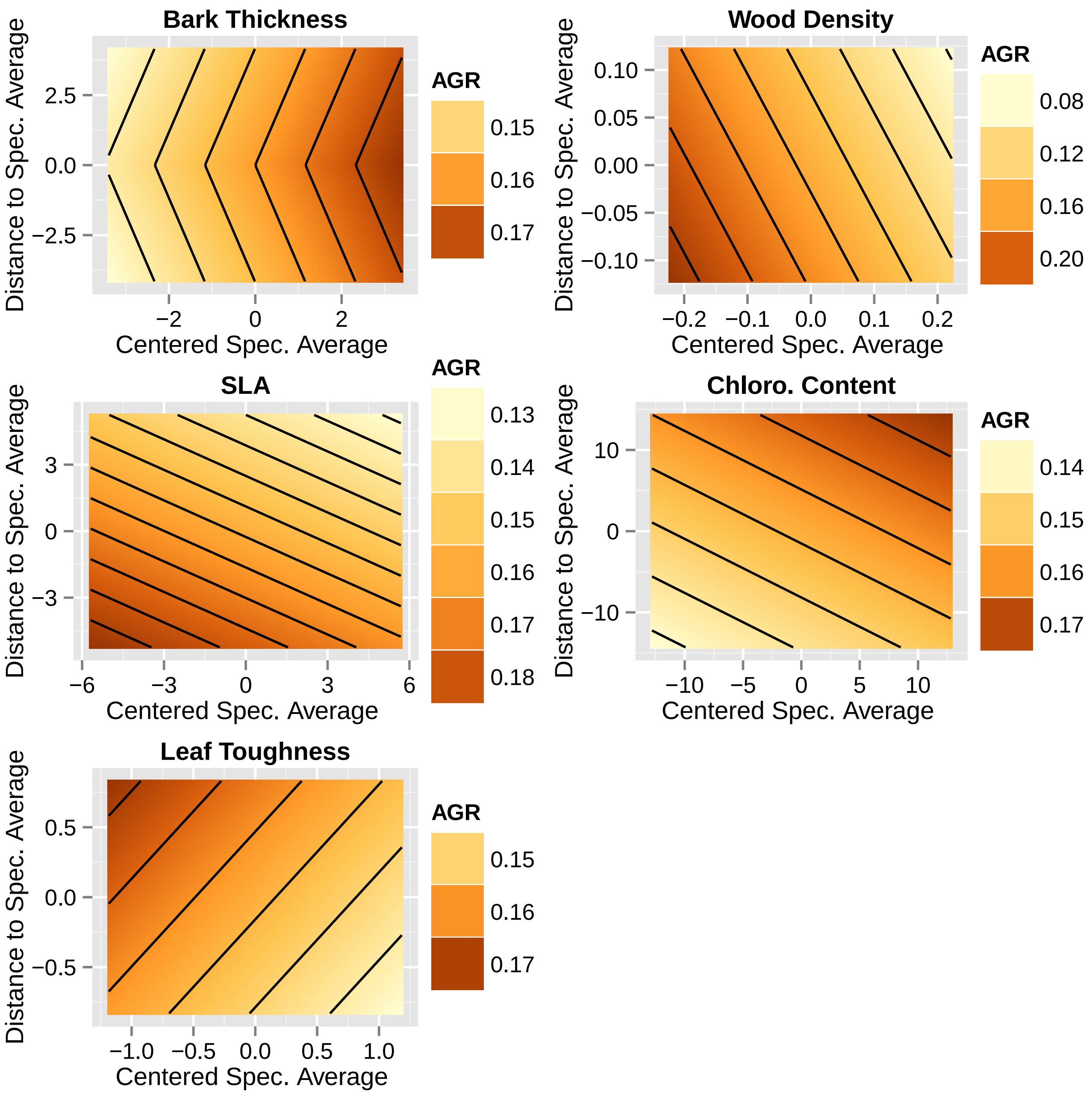

Figure 2: Simulations of species trait and predictions of AGR with growth models. Surface plots of predicted AGR of simulated range of data: X-axis, centered species average trait (species average trait minus mean of all species average trait); Y-axis, individual distance to species average trait. Black 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

We showed how in our data set of traits in neo-tropical forest, 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. 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.

For each trait independently, intra-specific variability has different effects on AGR. 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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