

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 → performance indexes → fitness, performance indexes reflect fitness, thus evolution. Linking functional traits and performance indexes → 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 variabilities.

Diameter Growth & Tropical Forests → French Guiana Context

Several growth models created, used → 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:

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

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)	$\text{cm}^2.\text{g}^{-1}$	Leaf economics	Individual Distance
Laminar total chlorophyll	$\mu\text{m}.\text{mm}^{-2}$	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 ; $\theta_0 \dots \theta_3$ 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: $\theta_4 \times \text{Tr}_s$ 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 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. 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.

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, it underlines that in our data set the micro-environment does not influence strongly the traits.

Explain pattern of variability, underlines importance of species effect for growth and trait **[missing figure]** However, species effect can't explain everything, tested for spatial auto-correlation.

Then, compared different growth models.

Examined link of predicted AGR with such model and distance to species average.

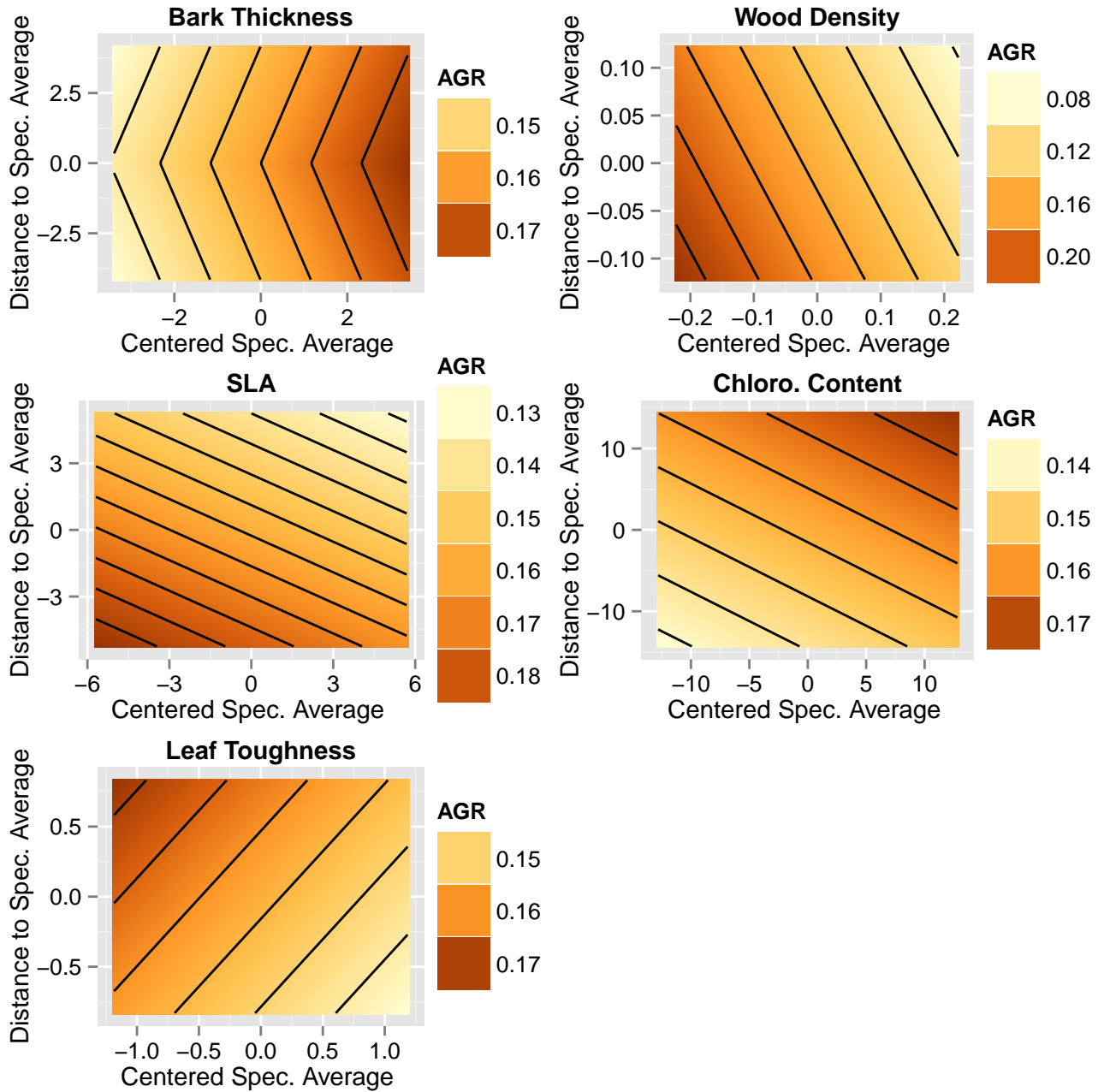


Figure 1: Simulations of species trait and predictions of AGR with growth models. Surface plots of predicted AGR of simulated range of data: X-axis, centered species average trait (species average trait minus mean of all species average trait); Y-axis, individual distance to species average trait. Black lines are equal-AGR lines over the surface. For traits detail see [Table 1](#).

Discussion

Authors Contributions and Acknowledgments

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