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]**.

Growth model

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

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

with $\epsilon_i \sim \mathcal{N}(0, \theta_3)$ the individual residual, where $\mathrm{AGR}_{i,s,p}$ 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 $\sigma^2_{0,s} \dots \sigma^2_{2,s}$ 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: $\theta_4 \times \mathrm{Tr}_s$ the species average value, with a parameter θ_4; $\theta_4 \times \mathrm{Tr}_s + \theta_5 \times (\mathrm{Tr}_i - \mathrm{Tr}_s)$ the distance of individual trait value Tr_i to species average, with the species term Tr_s; or $\theta_4 \times \mathrm{Tr}_s + \theta'_5 \times |\mathrm{Tr}_i - \mathrm{Tr}_s|$ the absolute distance to species average trait, with the species term Tr_s; or $\theta'_4 \times \mathrm{Tr}_i$ 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.

Trait Name	Units	Role
Trunk bark thickness	mm	Stem economics
Xylem density (wood density)	$g.cm^{-3}$	Stem economics
Specific Leaf Area (SLA)	$cm^2.g^{-1}$	Leaf economics
Laminar total chlorophyll	$\mu m.mm^{-2}$	Leaf economics
Laminar toughness	N	Leaf economics

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)

Data analysis

All data analyses were made using R Core Team (2015) version 3.2.0 (2015-04-16), plots were made with 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

Discussion

Authors Contributions and Acknowledgments

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