

## Summary

Functional Ecology aims to understand Ecology through functional traits. Those functional traits correlate with performance indexes. Radial growth is an easily measurable performance index, therefore abundant literature describes its evolution. Several statistical models have been made to predict radial growth using functional traits.

Several authors pointed out the importance of considering intra-specific variability in models to gain predictive performance. However, most growth models do not include intra-specific variability explicitly.

Here we focused on 9 1ha plots in French Guiana comprising a total of 3483 trees, having both traits and growth measurements. We contrasted the intra- and inter-specific variabilities of traits and growth and found that only 30% of the variance of growth was explained by the species effect. From what has been showed for competition we investigated how the relative position of an individual compared to its species average trait could affect performance. We compared growth model including species average, hierarchical distance, absolute distance, and individual trait terms. Including hierarchical distance or absolute distance in our growth model did not highly improve the performances of our growth model. However, depending on the trait, growth rate patterns showed how the same magnitude of variation in individual distance or in species average trait had different consequences on growth rate. For leaf toughness, increasing individual trait increased growth rate while increasing species average trait decreased growth rate.

Opposed effects on performance unravel trade-offs between intra- and inter-specific variabilities. For other studied traits, no such trade-offs were found indicating that other ecological mechanisms are involved in species trait equilibria.

## Introduction

Functional ecology aims to understand ecology through the core concept of functional trait (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 locations, species or individuals on their capacity to maintain biomass or the gene pool over generations. Focusing on functional traits also allowed to expand the historical concept of *ecological niche* from Hutchinson (1957), to the concept of *functional niche* (Violle and Jiang, 2009). It extended community ecology and sharpened understanding of community assemblages (Kraft and Ackerly, 2010). Several hypotheses were suggested to predict assemblages: competitive exclusion implies that more closely related individuals in traits experience greater competition than more distant ones, environmental filtering suggest that abiotic conditions (i.e. temperature, precipitation, etc.) select for certain types of traits in the community, Kunstler et al. (2012) instead suggested that the hierarchical trait difference between trees drove community assemblage in alpine forests.

Community dynamics, i.e. the change of community composition through time, can be studied through performance indexes. They should be comparable across species and environmental gradients to explain the variety of processes going on. It was assumed as underlined by McGill et al. (2006) that population increase rate was the best possible measure. In their review they argued that performance indexes should be easily measurable on a great number of species and connected to physiology, such as seed output or tree height, that reflect reproductive and light acquisition strategies respectively. Those performance indexes are related to population dynamics and they integrate various facets of them: growth vs. survival for example.

Radial growth is an example of performance currency for trees, it has been used in wide range of environmental gradients (Hérault et al., 2011; Kunstler et al., 2012). As radial growth is related to biomass production, it is a key parameter to understand the potential CO<sub>2</sub> sink that forests represent worldwide. Hérault et al. (2011) modeled radial growth from functional traits, making a highly generic model adapted to the various shapes that radial growth can take through ontogeny across tropical tree species. However, in their model, they did not consider intra-specific variability of traits, i.e. that the individuals of a

given species do not share the same traits; instead, in the model, individuals of a species have all the same traits equal to the species average value — intra-specific variability is not modeled explicitly.

Growing literature in functional ecology underline the importance of taking intra-specific variability into account both in trait values and performance in models (Violle and Jiang, 2009; Clark et al., 2010; Albert et al., 2011; Violle et al., 2012). Albert et al. (2011) still point out that intra-specific variability can be ignored if negligible compared to inter-specific variability. If not they underline that intra-specific variability in traits may have consequences on performance indexes. For example, a tree with a denser wood than its species average density may have a lower growth than its species average growth. Kunstler et al. (2012) showed how neighbors tree one of species  $A$  and the other one of species  $B$ , with trait  $t_A$  and  $t_B$  respectively, had their performances driven by their trait hierarchy  $t_A - t_B$ . For most traits, they showed that hierarchical distance ( $t_A - t_B$ ) better predicts performance than absolute traits distance  $|t_A - t_B|$ . Instead of making a hierarchy between to neighbors trees, we could position the traits of an individual tree compared to its species average value to unravel the interplay between inter-specific (the species' position) and intra-specific (the individual's position) variabilities and how they affect performance.

Using radial growth and traits data sets of 9 1ha plots spread over French Guiana (Baraloto et al., 2010) (Figure 1a) we wondered (i) how intra-specific variabilities are structured both in traits and in performance compared to inter-specific variabilities. (ii) Are those intra-specific variabilities due to the environment? (iii) Are intra- and inter-specific variabilities 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?

## 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 Figure 1a). In each plot, tree diameters 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 was a collection of five functional traits (see Table 1) extracted from a bigger database (Baraloto et al., 2010) on the same trees. Selected traits can be seen in two orthogonal axes of variations: leaf and stem economics spectra, contrasting different ecological strategies (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 (Coste et al., 2010). 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 (Chave et al., 2009). Trunk bark thickness associate with defense strategies in neotropical forests, thicker bark provides higher resistance to pathogens and herbivores (Paine et al., 2010).

## Statistical analyses

### How are intra-specific variabilities structured compared to inter-specific variabilities?

To understand how inter-specific variability contrasted with intra-specific variability, we partitioned the variance of each trait and performance using ANALyses Of VARIAnces (ANOVAs) with a species term as follow:

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

$$\text{AGR}_{s,i} = \overline{\text{AGR}_s} + \epsilon'_i, \quad (1b)$$

with  $\text{Tr}_{s,i}$ , the trait of individual  $i$  of species  $s$ ;  $\mu_s$  the mean trait of species  $s$ ;  $\epsilon_i$  the individual trait error term with a Gaussian distribution;  $\text{AGR}_{s,i}$  the AGR of individual  $i$  of species  $s$ ;  $\overline{\text{AGR}_s}$  the average AGR of species  $s$ ;  $\epsilon'_i$  the individual AGR error term and  $\epsilon_i \sim \mathcal{N}(0, \sigma^2)$ ,  $\epsilon'_i \sim \mathcal{N}(0, \sigma'^2)$ . 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 plus white noise. We partitioned the variance similarly for AGR.

### How does trait intra-specific variability influence radial growth?

In order to understand the influence of trait intra-specific variability on radial growth, we modeled AGR with a mixed linear model of traits and other factors. Based on Hérault et al. (2011) ontogenical model, we used fixed terms  $DBH$  and  $\log(DBH)$ , because they capture well the hump shape of growth during ontogeny for tropical trees. As they did, we modeled  $\log(AGR + 1)$  because of data high heteroscedasticity. We added a random intercept for species effect to take inter-specific variability into account, this effect also influenced the slopes of  $DBH$  and  $\log(DBH)$  terms. We also added a random intercept plot effect to take inter-plot variability into account.

Then depending on the hypothesis tested various fixed terms were added to the model:

$$\begin{aligned} \log(\text{AGR}_{p,s,i} + 1) = & {}^0\theta + {}^0\gamma_s + \gamma_p \\ & + ({}^1\theta + {}^1\gamma_s) \times \text{DBH} \\ & + ({}^2\theta + {}^2\gamma_s) \times \log(\text{DBH}) \\ & + \delta + \epsilon_i, \end{aligned} \quad (2)$$

with  $\epsilon_i \sim \mathcal{N}(0, {}^3\theta)$  the individual residual, where  $\text{AGR}_{p,s,i}$  is the AGR of tree  $i$  of species  $s$  in plot  $p$ ;  ${}^0\theta \dots {}^3\theta$  are parameters to be estimated;  ${}^0\gamma_s \dots {}^2\gamma_s$  and  $\gamma_p$  follow a zero-centered Gaussian distribution with unknown variances  ${}^0\sigma_s^2 \dots {}^2\sigma_s^2$  and  $\sigma_p^2$ .  $\text{Tr}_s$  is the average trait value for species  $s$ .

We tested different hypotheses through the  $\delta$  term in Equation 2. If we position an individual relative to its species mean, we can compare them on a hierarchy of traits, and the relevant variable is the hierarchical distance between individual trait and species average trait. We may also hypothesized as Kunstler et al. (2012) did for competition, that the relevant relation for AGR would be the absolute distance. We obtain two models that have to be compared with models having only the specific trait or the individual trait.

$$\delta = \begin{cases} {}^4\theta \times \text{Tr}_s & \text{Species Average} \\ {}^4\theta \times \text{Tr}_s + {}^5\theta \times (\text{Tr}_i - \text{Tr}_s) & \text{Hierarchical Dist.} \\ {}^4\theta \times \text{Tr}_s + {}^5\theta' \times |\text{Tr}_i - \text{Tr}_s| & \text{Absolute Dist.} \\ {}^4\theta' \times \text{Tr}_i & \text{Individual Trait} \end{cases} \quad (3)$$

$\text{Tr}_s$  the species average value, with a parameter  ${}^4\theta$ ;  $\text{Tr}_i - \text{Tr}_s$  the hierarchical distance of individual trait value  $\text{Tr}_i$  to species average trait value  $\text{Tr}_s$ ; or  $|\text{Tr}_i - \text{Tr}_s|$  the absolute distance to species average trait; and  $\text{Tr}_i$  the individual trait value.

### Intra-specific variability vs. inter-specific variability effects on performance for each trait

Intra-specific variability and inter-specific variability may have different impacts on performance. For each trait we selected the growth model from Equation 3 that had the highest adapted R-squared for mixed models (Nakagawa and Schielzeth, 2013), i.e. the model that best described our data. Using them we predicted AGR based on a 5%-95% range of species average and hierarchical distance.

## 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

We partitioned variance due to the species effect, i.e. the part of the variance explained by the species of individuals (see Figure 1b). 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.

To test how growth was affected by individual traits we made growth mixed-model for each one of them (see Table 1 for traits and Table 2 for models) as predictors of the AGR. Based on the adapted R-squared for mixed-models (Nakagawa and Schielzeth, 2013), we selected the best model for each trait (see Table 2).

For all traits models with distance measures were better than model with only species average term. But for wood density and SLA, hierarchical distances model performed as well as individual's trait models. By adding a distance term to the species average term model, we gained in predictive power, shown by the increase of condition R-squared between models.

For bark thickness the absolute distance model improved the conditional R-squared by 0.025 compared to the model with only species average trait. For wood density hierarchical distance model improved the R-squared by 0.056 (10% of total  $R^2$ ) compared to species average model. While for SLA hierarchical distance model only increased  $R^2$  by 0.004. For laminar chlorophyll and toughness the hierarchical distance models gained 0.001 of R-squared compared to the species average term models.

Using the best models (in bold in Table 2) that included a distance term we predicted AGR for a range of individual trait values and species av-

erage values. To underline the interplay between intra- and inter-specific variabilities we plotted the centered species average trait value vs. the hierarchical distance of individual's (see Figure 2). We obtained AGR "landscapes", that show the pattern of variations of variation as a function of individual and species trait variation. Depending on the trait we had different patterns, for SLA and wood density we had similar patterns: the larger the species average trait value, the lower the AGR, and the higher the individual hierarchical distance the lower the AGR. For example, an increase of  $10\text{cm}^2.\text{g}^{-1}$  in SLA species average decreases the growth by  $0.035\text{mm}.\text{yr}^{-1}$  while the same increase in hierarchical distance decreases the AGR by  $0.02\text{mm}.\text{yr}^{-1}$ . For laminar chlorophyll content we observe that increasing species average as well as increasing hierarchical distance lead to increasing AGR. While for leaf toughness, species average and hierarchical AGR gradients are opposed: an increase in species average decreases AGR, and an increase individual hierarchical distance increases AGR. Because the best model for bark thickness was an absolute distance model, we observe the symmetrical patterns of AGR variations for change in hierarchical distance: globally, the higher the hierarchical distance the lower the AGR, while the higher the species average, the lower the growth.

## Discussion

From our data set we showed that taking into account intra-specific variability does not improve much the performance of growth models; given the extent of sampling needed to measure individual traits. However, we showed how individual trait value had implications on tree performance when compared to its species average trait. The same magnitude of variation in trait value impacted performance differently if it affected intra- or inter-specific variabilities.

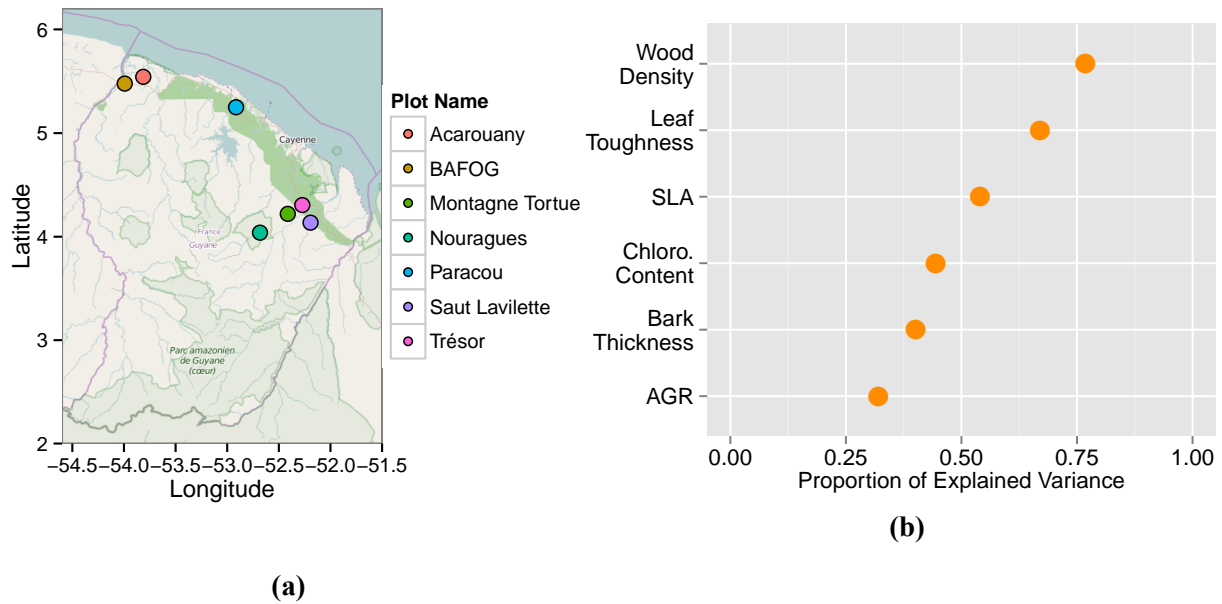
### Taking intra-specific variability into account in growth model

Taking intra-specific variability into account has been a running debate in functional ecology, it is a trade-off between the cost of sampling sev-



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



**Figure 1: (a) Plots map.** 9 1-ha plots were used, spread in French Guiana, two plots were surveyed both in Nouragues and in Paracou (see Baraloto et al., 2010) **(b) Explained variance by species effect in ANOVAs.** Dot-plot of explained variance in ANOVA by the species effect for traits and AGR. **Chloro. Content:** Laminar Chlorophyll Content, **AGR:** Annual Growth Rate (in diameter).

eral individuals per species and the information gained by such sampling (Albert et al., 2011; Violle et al., 2012). Indeed, in our data set, for radial growth, it seemed reasonable to link intra-specific growth variability to traits intra-specific variabilities; however, we have shown here that those variabilities are only slightly related. For wood density or bark thickness, the use of hierarchical distance improved the prediction by around a 10% factor in R-squared, while for the other traits it was less than a factor 1% in R-squared. 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 highly affect

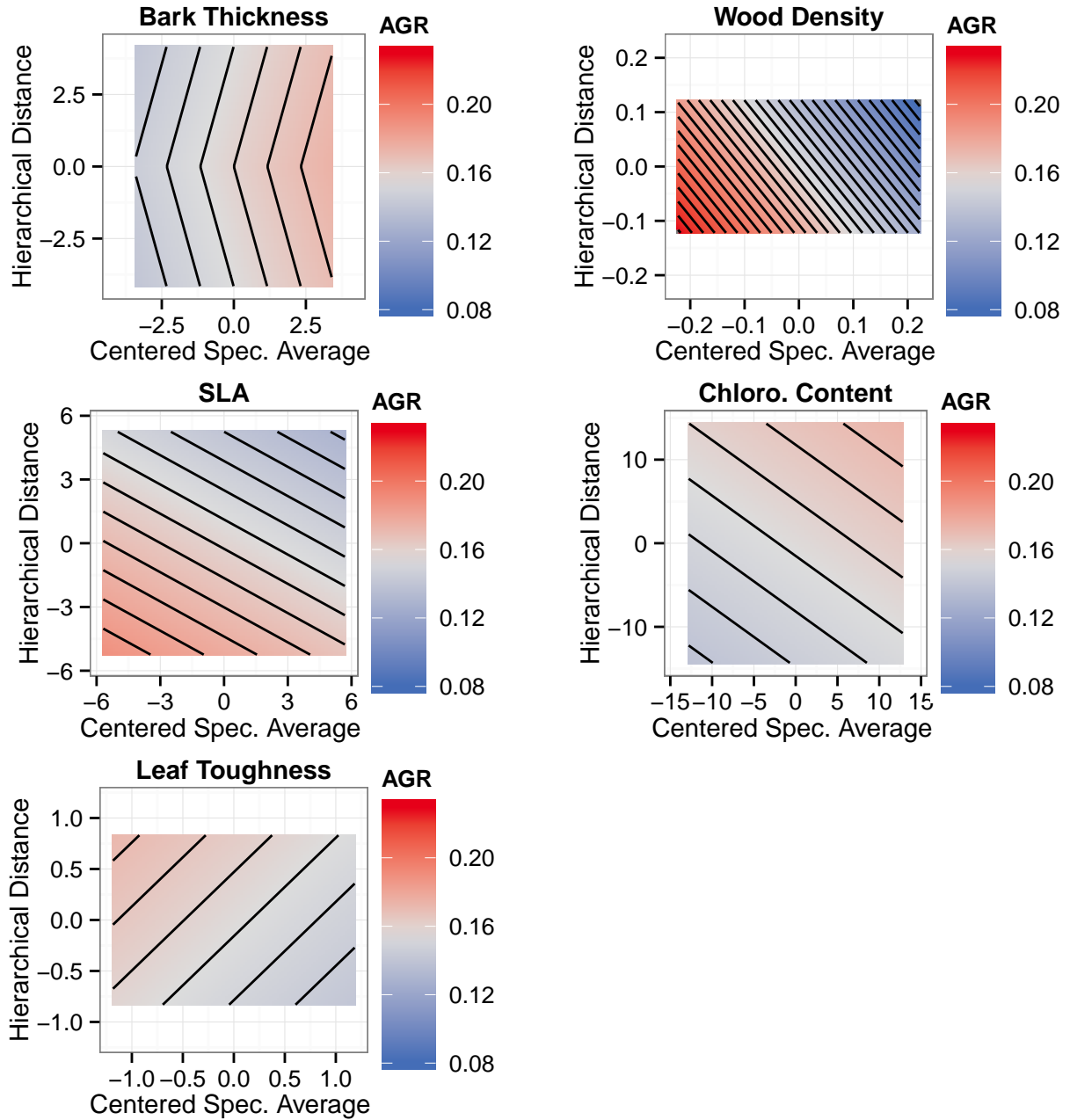
predictive performances.

## Variabilities in radial growth and traits

We showed that traits and growth intra-specific variabilities do not seem to correlate well in our case. Several causes may however explain those variabilities. Micro-environmental variations may cause each individual to exhibits variations in AGR or traits and lead to intra-specific variability. However, we saw no spatial autocorrelation in traits (data not shown) nor in growth model residuals. Albert et al. (2010) suggested that genetic structure between different popula-

Trait Name	Model Type	Marginal R <sup>2</sup>	Cond. R <sup>2</sup>	AIC	logLikelihood
Bark Thickness	Species Avg.	0.104	0.472	-2790	1407
	Hierarchical Distance	0.106	0.471	-2794	1410
	<b>Absolute Distance</b>	0.100	<b>0.497</b>	-2860	<b>1443</b>
	Individual Trait	0.102	0.470	-2792	1408
Wood Density	Species Avg.	0.142	0.474	-1838	931
	<b>Hierarchical Distance</b>	0.139	<b>0.530</b>	-1910	<b>968</b>
	Absolute Distance	0.140	0.529	-1906	966
	<b>Individual Trait</b>	0.137	<b>0.530</b>	-1911	<b>968</b>
SLA	Species Avg.	0.094	0.485	-3081	1553
	<b>Hierarchical Distance</b>	0.095	<b>0.489</b>	-3092	<b>1559</b>
	Absolute Distance	0.096	0.459	-3000	1513
	<b>Individual Trait</b>	0.096	<b>0.490</b>	-3093	<b>1559</b>
Chloro. Content	Species Avg.	0.092	0.487	-3143	1583
	<b>Hierarchical Distance</b>	0.093	<b>0.488</b>	-3145	<b>1586</b>
	Absolute Distance	0.092	0.486	-3143	1584
	Individual Trait	0.100	0.469	-3075	1550
Toughness	Species Avg.	0.088	0.478	-3136	1580
	<b>Hierarchical Distance</b>	0.088	<b>0.479</b>	-3135	<b>1581</b>
	Absolute Distance	0.088	0.478	-3134	1580
	Individual Trait	0.088	0.479	-3134	1579
All Traits	Species Avg.	0.133	0.524	-1739	885
	<b>Hierarchical Distance</b>	0.143	<b>0.532</b>	-1761	<b>901</b>
	Absolute Distance	0.138	0.524	-1743	892
	Individual Trait	0.138	0.528	-1766	899

**Table 2: Summary table of tested trait-specific growth models.** We modeled radial growth using linear-mixed model, all models contained plot and species random effects, as well as DBH and log DBH terms to take growth curve shape into account (Héroult et al., 2011). Then, for each trait, we added a fixed effect that contained different terms: **Species Avg.**, only the species average trait value; **Hierarchical Distance**, the species average plus the difference between individual trait and species average; **Absolute Distance**, the species average plus the absolute difference between individual trait and species average; **Individual Trait**, only the trait value of individuals. Models indicated in **bold** are those with the highest logarithmic likelihood per trait. Not all traits had been measured on each tree, giving a different number of comprised tree for each model, thus the likelihood of models for each trait are not comparable.



**Figure 2: Predictions of AGR depending on intra-specific and inter-specific variabilities in traits.** 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, each line mark a  $5e^{-3} \text{mm.yr}^{-1}$  break. For details on traits see [Table 1](#).

tions of the same species could structure traits intra-specific variability: sub-populations may be genetically more related inside themselves than between them, having traits more similar inside the same sub-population.

## Interplay of inter-specific and intra-specific trait variabilities

Intra- vs. inter-specific trait variabilities affect AGR patterns differently. We have shown using performance landscapes (see [Figure 2](#)) that for each trait a variation in hierarchical distance or the same variation in species average had different consequences on performance. We underlined very diverse patterns of variations depending on the trait used. However, those patterns suggest striking interpretation: for example a continuous decrease in wood density seems to highly increase AGR. Trees, still, do not decrease their wood density as such. Radial growth is a performance index related mainly to tree survival ([Aubry-Kientz et al., 2015](#)) and not to fitness, it does not indicate the evolutionary path that an individual follows. Instead, radial growth gives us insight on the ecological strategy of a species, either being a fast or a slow growing species. The fact that we do not observe decreasing wood density in time also suggest that other phenomena could limit this decrease. Wood density is a key trait that experience several trade-offs ([Chave et al., 2009](#)) because of mechanical stresses or defence against herbivory that constrain its value.

Leaf toughness exhibits another contrasted pattern where increasing hierarchical distance increases AGR while increasing species average trait decreases AGR. Here intra-specific and inter-specific variabilities are in opposite direction, this may lead to a species wide trade-off for AGR that could constrain leaf toughness values. In this case, because of opposite dynamics at the individual and species levels for a trait, the trait could reach a stable equilibrium. What may influence such an equilibrium if it exists? Is it stable over time? Species functional niches are considered stable over time, overseeing the dynamics of such spaces.

While intra-specific variability has been shown to influence community assembly, implementing it in growth model on our data sets does not

highly improve the predictive performance. However, the equilibrium between intra-specific and inter-specific variabilities to achieve higher performance may play a role in community assembly. More investigations are needed to unravel the interplay between inter- and intra-specific variabilities.

## Authors Contributions and Acknowledgments

## References

- Albert, C. H., Grassein, F., Schurr, F. M., Vieilledent, G. and Violle, C. (2011). When and how should intraspecific variability be considered in trait-based plant ecology? *Perspectives in Plant Ecology, Evolution and Systematics* *13*, 217--225.
- Albert, C. H., Thuiller, W., Yoccoz, N. G., Soudant, A., Boucher, F., Saccone, P. and Lavorel, S. (2010). Intraspecific functional variability: extent, structure and sources of variation. *Journal of Ecology* *98*, 604--613.
- Aubry-Kientz, M., Rossi, V., Boreux, J.-J. and Hérault, B. (2015). A joint individual-based model coupling growth and mortality reveals that tree vigor is a key component of tropical forest dynamics. *Ecology and Evolution* .
- Baraloto, C., Timothy Paine, C. E., Poorter, L., Beauchene, J., Bonal, D., Domenach, A.-M., Hérault, B., Patiño, S., Roggy, J.-C. and Chave, J. (2010). Decoupled leaf and stem economics in rain forest trees. *Ecology Letters* *13*, 1338--1347.
- Bartoń, K. (2015). MuMIn: Multi-Model Inference. R package version 1.13.4.
- Bates, D., Mächler, M., Bolker, B. and Walker, S. (2014). Fitting Linear Mixed-Effects Models using lme4. *arXiv:1406.5823 [stat]* .
- Chave, J., Coomes, D., Jansen, S., Lewis, S. L., Swenson, N. G. and Zanne, A. E. (2009). Towards a worldwide wood economics spectrum. *Ecology Letters* *12*, 351--366.



- Clark, J. S., Bell, D., Chu, C., Courbaud, B., Dietze, M., Hersh, M., HilleRisLambers, J., Ibáñez, I., LaDeau, S., McMahon, S. and others (2010). High-dimensional coexistence based on individual variation: a synthesis of evidence. *Ecological Monographs* 80, 569--608.
- Coste, S., Baraloto, C., Leroy, C., Marcon, □., Renaud, A., Richardson, A. D., Roggy, J.-C., Schimann, H., Uddling, J. and Hérault, B. (2010). Assessing foliar chlorophyll contents with the SPAD-502 chlorophyll meter: a calibration test with thirteen tree species of tropical rainforest in French Guiana. *Ann. For. Sci.* 67, 607--607.
- Hutchinson, G. E. (1957). Concluding Remarks. *Cold Spring Harb Symp Quant Biol* 22, 415--427.
- Hérault, B., Bachelot, B., Poorter, L., Rossi, V., Bongers, F., Chave, J., Paine, C. E. T., Wagner, F. and Baraloto, C. (2011). Functional traits shape ontogenetic growth trajectories of rain forest tree species: Plant traits shape growth trajectory. *Journal of Ecology* 99, 1431--1440.
- Kraft, N. J. and Ackerly, D. D. (2010). Functional trait and phylogenetic tests of community assembly across spatial scales in an Amazonian forest. *Ecological Monographs* 80, 401--422.
- Kunstler, G., Lavergne, S., Courbaud, B., Thuiller, W., Vieilledent, G., Zimmermann, N. E., Kattge, J. and Coomes, D. A. (2012). Competitive interactions between forest trees are driven by species' trait hierarchy, not phylogenetic or functional similarity: implications for forest community assembly. *Ecol Lett* 15, 831--840.
- McGill, B. J., Enquist, B. J., Weiher, E. and Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution* 21, 178--185.
- Nakagawa, S. and Schielzeth, H. (2013). A general and simple method for obtaining R<sup>2</sup> from generalized linear mixed-effects models. *Methods Ecol Evol* 4, 133--142.
- Paine, C. E. T., Stahl, C., Courtois, E. A., Patiño, S., Sarmiento, C. and Baraloto, C. (2010). Functional explanations for variation in bark thickness in tropical rain forest trees. *Functional Ecology* 24, 1202--1210.
- R Core Team (2015). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing Vienna, Austria.
- Violle, C., Enquist, B. J., McGill, B. J., Jiang, L., Albert, C. H., Hulshof, C., Jung, V. and Messier, J. (2012). The return of the variance: intraspecific variability in community ecology. *Trends in Ecology & Evolution* 27, 244--252.
- Violle, C. and Jiang, L. (2009). Towards a trait-based quantification of species niche. *J Plant Ecol* 2, 87--93.
- Westoby, M. (1998). A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil* 199, 213--227.
- Wickham, H. (2009). *ggplot2: elegant graphics for data analysis*. Springer New York.