Summary

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_2 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 considered 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-specifc 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) we wandered (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 environ-

ment? (iii) Are intra- and inter- specific variaiblities 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, 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 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. 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).

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:

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

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

with $\text{Tr}_{s,i}$, the trait of individual i of species s; μ_s the mean trait of species s; ϵ_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; ϵ'_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. 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 linear-mixed of traits and other factors. Based on Hérault et al. (2011) 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 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:

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

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; ${}^0\theta \ldots {}^3\theta$ are parameters to be estimated; ${}^0\gamma_s \ldots {}^2\gamma_s$ and γ_p follow a centered Gaussian distribution with unknown variances ${}^0\sigma_s^2 \ldots {}^2\sigma_s^2$ and σ_p^2. Tr_s is the average trait value for species s.

We tested different hypotheses through the δ 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.

$$\delta = \begin{cases} {}^4\theta \times \text{Tr}_s \\ {}^4\theta \times \text{Tr}_s + {}^5\theta \times (\text{Tr}_i - \text{Tr}_s) \\ {}^4\theta \times \text{Tr}_s + {}^5\theta' \times |\text{Tr}_i - \text{Tr}_s| \\ {}^4\theta' \times \text{Tr}_i \end{cases} \quad (3)$$

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

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

Intra-specific variability and inter-specific variaibilty 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. 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 selected trait-specific models with DBH set as data median value.

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 and Absolute distances models had similar performances.

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 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. 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
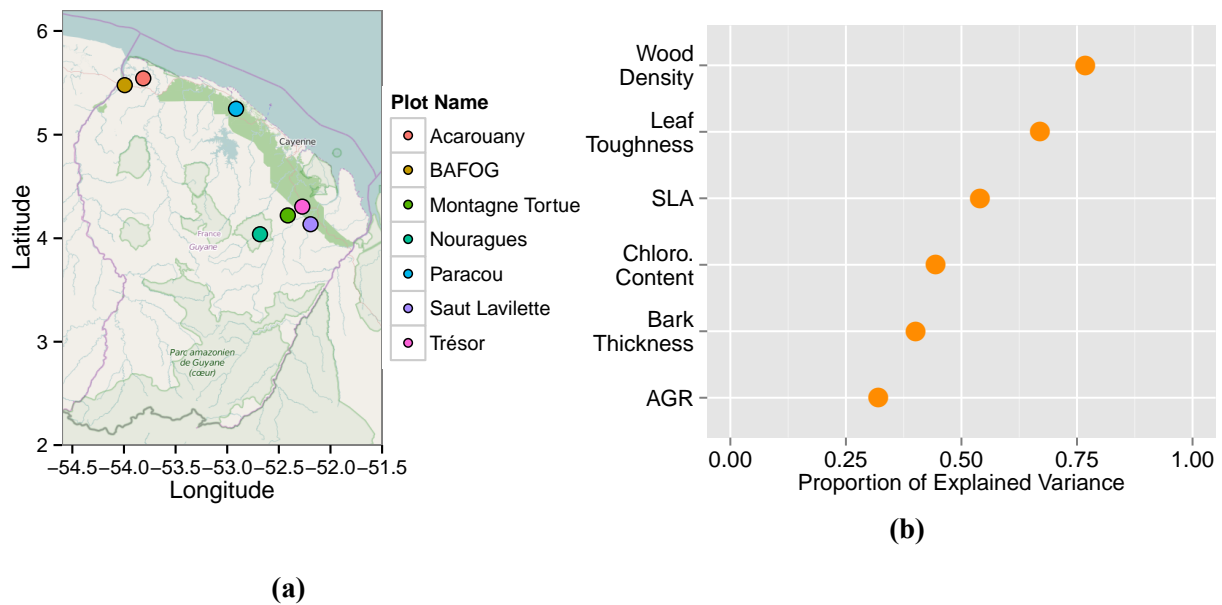
(a)

(b)

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. The right space after the orange is the residual variance. **Chloro. Content**: Laminar Chlorophyll Content, **AGR**: Annual Growth Rate (in diameter).

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.

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.

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

Trait Name	Model Type	Marginal R^2	Cond. R^2	AIC	logLikelihood
Bark Thick.	Species Avg.	0.104	0.472	-2790	1407
	Hierarchical Distance	0.106	0.471	-2794	1410
	Absolute Distance	0.100	**0.497**	-2860	**1443**
	Individual Trait	0.102	0.470	-2792	1408
Wood Density	Species Avg.	0.142	0.474	-1838	931
	Hierarchical Distance	0.139	**0.530**	-1910	**968**
	Absolute Distance	0.140	0.529	-1906	966
	Individual Trait	0.137	**0.530**	-1911	**968**
SLA	Species Avg.	0.094	0.485	-3081	1553
	Hierarchical Distance	0.095	**0.489**	-3092	**1559**
	Absolute Distance	0.096	0.459	-3000	1513
	Individual Trait	0.096	**0.490**	-3093	**1559**
Chloro. Content	Species Avg.	0.092	0.487	-3143	1583
	Hierarchical Distance	0.093	**0.488**	-3145	**1586**
	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
	Hierarchical Distance	0.088	**0.479**	-3135	**1581**
	Absolute Distance	0.088	0.478	-3134	1580
	Individual Trait	0.088	0.479	-3134	1579

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 (Hérault 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's trait and species average; **Absolute Distance**, the species average plus the absolute difference between individual's 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.

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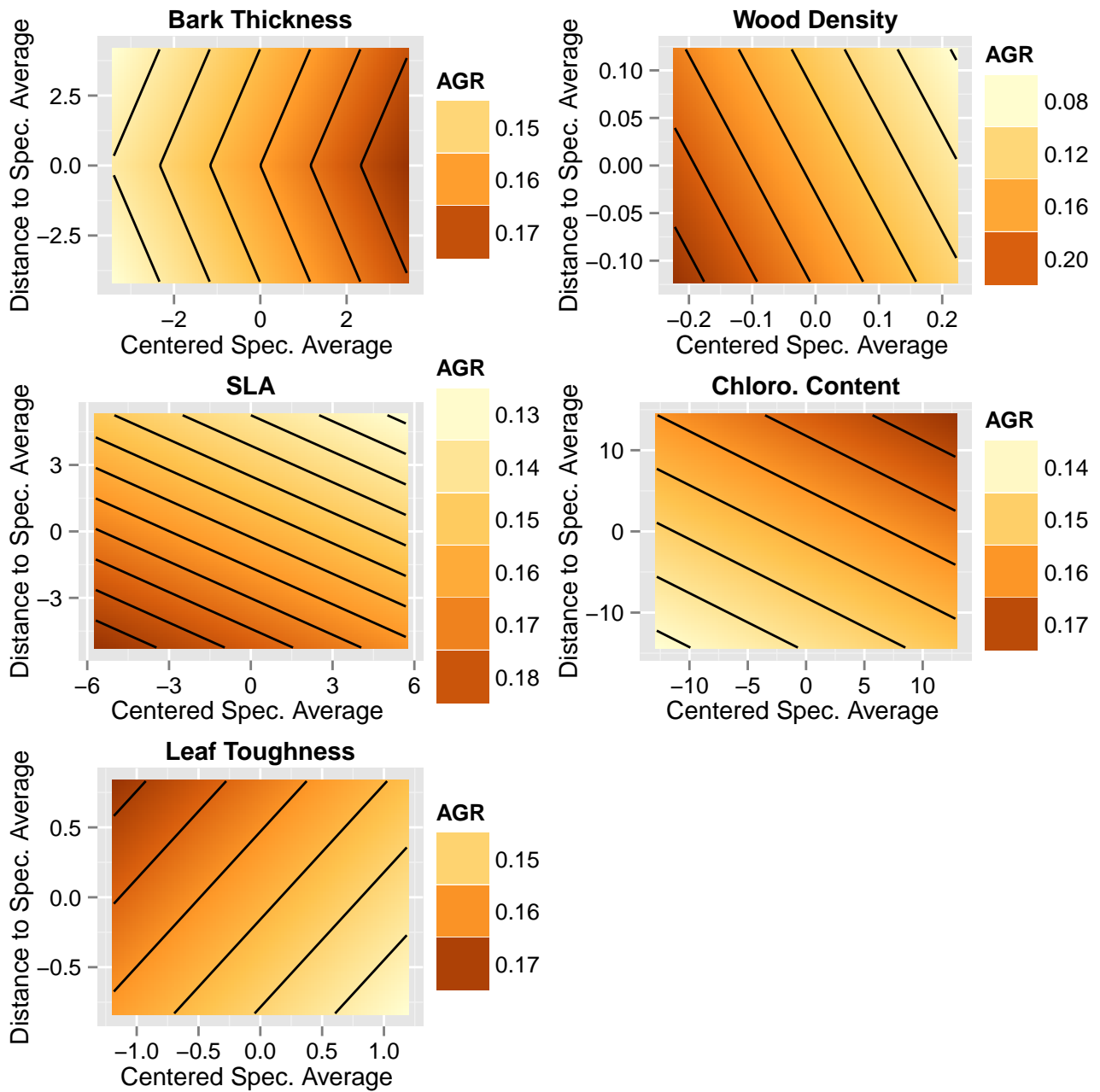
Figure 2: Simulations of species trait and predictions of AGR with growth models. Surface plots of predicted AGR of simulated range of data: X-axis, centered species average trait (species average trait minus mean of all species average trait); Y-axis, individual distance to species average trait. Black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

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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