

The scientific content of the article is interesting and straightforward, with stimulating discussions and perspectives for ecologists.

My main suggestions concern 1) the writing of the introduction, 2) a suggestion to discuss the proxies of environmental variables, and 3) the comments on Clark 2010 in the discussion. Otherwise, I have many minor comments on the phrasing or the presentation.

### **1) Introduction**

Overall, all elements are interesting and justified but need to be better articulated; maybe using transition phrases between paragraphs and even sometimes between sentences.

I show below how I understood the discourse of the introduction to demonstrate how it could be made easier to follow for the reader.

#### **First paragraph**

*1) Individual growth = determinant of species performance + driver of forest dynamics & composition → understanding its determinants is important to predict the trajectories of tropical forests in the context of anthropogenic disturbances.*

This first block is OK for me.

*2) Tree growth plays a role in species ecological strategies through demographic trade-offs e.g. growth-mortality trade-offs → details about this trade-off.*

OK but reformulate to make it smoother. For instance line 51 we need a transition to make it clear and elegant that you develop the growth-mortality trade-off you just introduced (for instance, “in this trade-offs, fast growing species...”).

*3) Efforts being made to forecast tropical forests dynamics by predicting the growth of species → functional traits → definition → expected to play a role in species growth → examples (wood density, max diameter, etc.)*

I feel like this block needs small changes to be clearer. Here are some suggestions.

- 1.54 I would add a connector like “hence”, and 1.55 I would not repeat “to predict the growth of species”  
*e.g. “Hence, in order to forecast the dynamics of tropical species, efforts have been made to predict the growth of species. For this purpose, functional traits have been widely explored and used (refs).”*
- 1.57 syntax: “traits that impact fitness” OR “trait that have an impact on”.  
I would add “indeed” before the definition of functional traits
- 1.58 remove “defined as” or change to “individual performance *i.e.* ...”
- 1.59 change “functional traits” to “they”
- 1.60 add “For instance”

#### **Second paragraph**

- I feel like this second paragraph describes a second kind of “effort that has been made to predict the growth of species”. Maybe you could clarify that you start a list? For instance by breaking the first paragraph in two after 1.55 (“Efforts have been made to predict the growth

of species”), or by adding “for instance” / “another trail” / “in parallel” /etc. each time you develop another aspect of the exploration of the prediction of species growth?

- 1.67 “The role of light has [notably or for instance] been ...”
- 1.74 it is unclear to me if you mean that the successional niches enable different species to take turns, or if you are talking about natural selection that produced all these strategies.
- 1.75 maybe precise that you consider the fast-slow continuum
- 1.77 you say that soil also determines species distribution, but you did not talk explicitly about species distribution earlier. Maybe precise that gap dynamics determines species distributions in space and time? For instance by moving 1.78 to the beginning “Species distribution is also driven by environmental variables, shaping indirectly the structure of the community.” and then develop light and soil.
- I also feel like the whole paragraph focuses on light but you add soil (water and nutrients) at the end. Maybe you could make obvious that the first paragraph (or second depending if you cut the first paragraph before detailing functional traits as suggested) is about species traits while the second is about the environmental determinants of species growth?

### **Third paragraph**

- Here you introduce intraspecific variability. To me it’s a crucial point of the introduction! I would at least add a “However” (or “Nevertheless” to avoid repetition) to show that you now shift perspective, or add “shifting on the individual level, ...”
- 1.85 I do not understand why you used “indeed”: are you making the supposition that, because species functional traits are poor predictors of individual response, biotic and abiotic environmental aspects must play a role in it?
- 1.87 do you have a reference?
- 1.89 “while the species-based approach..., the individual approach focuses” (do not forget the second “focuses”).
- 1.90 to 110: you enumerate example of ways individual growth can be mediated. Make that clear by announcing it before. For example you could use the phrase “There are many factors shaping the growth of individuals within species” and then “notably/in particular gap dynamics” or “an important one is gap dynamics”.

### **Fourth paragraph**

The structure is OK for me.

- 1.113 “for across”? Syntax problem here (I guess it is just “across”)
- 1.115 maybe change “and” to “,”

### **Fifth paragraph**

This is crystal clear to me!

## **2) A suggestion to discuss environmental proxies**

1.363-369: could you (quickly) discuss the scale of the environmental variables vs. the individual scale (particularly for TWI although 1 m is a good resolution) + are your variables good proxies of local environmental conditions (particularly how good a proxy is elevation for plant water availability) + the effect of past environmental conditions that are not captured but impact the long-term growth strategy of the individual?

## **3) About Clark 2010 and hypotheses on the effect of intraspecific variability on species coexistence**

- You cite Clark (2010) but in your bibliography we find Clark *et al.* (2010, *Ecological Monographs*), which is much longer and less “iconic”. I will now comment as if you really meant Clark (2010, *Science*).
- 1.461-465: That is not Clark's main message. See Stump *et al.* (2021, *Ecological Monographs*) for a clear summary of the essence of Clark (2010). Clark (2010) on the contrary shows that although individuals within species apparently differ greatly in their performances, conspecifics still respond more similarly to environmental variation than heterospecifics. Observed intraspecific variation is merely the reflection of species' high dimensional response to environmental variation. He does not present intraspecific variation as a mechanism enabling species coexistence; the only coexistence mechanism presented in his reflection framework is species differentiation in many niche dimensions coupled with biotic and abiotic environmental variation in many dimensions. The link with intraspecific vs. interspecific competition would not work otherwise: coexistence is stabilised because conspecifics respond more similarly than heterospecifics in the same environmental conditions, thus enabling higher intra- than interspecific competition, which stabilises coexistence (Chesson 2000).
- However, Clark (2010) along with other pieces of work (Clark *et al.* 2010; Clark *et al.* 2007, *Ecology Letters*) is often cited as a study showing a positive effect of intraspecific variability on species coexistence (e.g. Hart *et al.* 2016, *Ecology Letters*; Uriarte *et al.* 2018, *Ecology Letters*; Westerband; Funk and Barton 2021, *Annals of Botany*). This corpus has further been classified outside of niche theory, as "individual variation theory", which explicitly identifies intraspecific variation as the main driver of local diversity (Violle *et al.* 2012, *Trends in Ecology and Evolution*; Bastias *et al.* 2017, *Plos One*; Crawford *et al.* 2019, *Oikos*; Westerband, Funk and Barton 2021). Yet, some other studies put this corpus back in the context of niche multidimensionality (e.g. Le Bec *et al.* 2015, *Plos One*; Banitz 2019, *Oikos*; Stump *et al.* 2021). Particularly, Stump *et al.* (2021) provide a clear summary of the core concept of Clark (2010). Indeed, they understood that the paper "argued that species coexist via high-dimensional niches, and proposed a test that used variability in growth and reproduction between individuals to detect such species-level differences.", and that the individual level "reveal species-level differences in the response to environmental variation."
- The hypothesis that intraspecific variability promotes coexistence by enabling local competitive hierarchy inversions exists though, but is presented in other works like Fridley *et al.* (2007, *Journal of Ecology*), Vieilledent *et al.* (2010, *Oecologia*) or more generally neutral theory.
- You should maybe present other hypotheses or at least note that other hypotheses exist. An alternative hypothesis is that intraspecific variability leads to niche overlap (“blurs” species differences) which leads to competitive exclusion (harm species coexistence). However, the same effect could destabilise species coexistence, leading to neutral dynamics and therefore promote transient coexistence. See the introductions of Lichstein *et al.* (2007) and of Hart *et al.* (2016) to have a general understanding of these opposing hypotheses. See also potentially Hart *et al.* (2016), Courbaud *et al.* (2012) and the synthesis of Stump *et al.* (2021) on the effect of non-linear averaging.

#### **4) General remarks and details**

##### **General**

- Make sure that the presentation of your **references** is homogeneous (*et al.* should be always in italics or always regular).  
1.78 Kupers (you forgot the “s”), 1.338 de Aguiar-Campos *et al.*, 20201 (date problem) → check all references, maybe using a reference manager like Zotero within Word or using LaTeX/Rmarkdown reference system?
- Control each item of you **Bibliography**: there are suspension points, squares in place of special characters, the journal names are not always in italics, the doi url is sometimes absent or is not highlighted as a url, there is a month (June).
- Choose between **British and American English**: “-ised”, “-ise” (BE) or “-ized”, “ize” (AE), “metres” or “meters”, “neighbour” or “neighbor”, *etc.*
- Search and replace double spaces, spaces before dots or after parentheses, absence of space after comma...
- Use consistent separators for big numbers (commas like 1.133 or spaces like 1.252), and make sure it is the case for all numbers above 999.
- Justify text
- Distinguish legend text from body text, and within legends distinguish the title.
- Make the space between the same heading level and the text consistent (*e.g.* Acknowledgments and Funding).

## **Materials & Methods**

### *Study site*

OK

- 1.151 Make sure one can say “in” the Guiana Shield (it could be “on” or “in the Guiana Shield region”).

### *Species and individuals*

OK

- 1.165 “and( iii)” → “and (iii)”

### *Individual growth*

- 1.162 We first explored with a reduced dataset the best model shape → We first used a reduced dataset to explore...
- 1.176 after describing verbally the model: maybe add “as detailed hereafter” (to reassure readers who did not understand the sentence that everything will be explained). But that could be inelegant.
- 1.180 and 185 strange blank spaces after the sigmas
- 1.188  $H(i,t)$  →  $DBH(i,t)$
- in the two last formulas + 1.189 change  $DBH_0(i)$  to  $DBH(i,0)$  for consistency with  $DBH(i,t)$
- 1.189 maybe change “a model can be fitted to predict annual individual diameter  $DBH(i,t)$  with observed diameter from censuses” to “a model can be fitted to observed diameters from censuses using a Gaussian distribution in order to predict annual individual diameter  $DBH(i,t)$  “
- 1.190 “Guassian” → “Gaussian”
- in the two last formulas: can you reduce the space between the sum and its content?
- 1.193 “in particular individual growth potential” → Why in particular? Either develop or remove.

## *Descriptors of individual growth potential*

### 1) NCI

- choose “20 m” or “20 metres” throughout the study
- 1.206 be consistent with the equation and choose between 0.25 and  $\frac{1}{4}$ .
- 1.206 I did not understand the explanation on the 0.25 parameter. Is it because  $\frac{1}{20} * \frac{1}{4}$  approaches 1%? If not, you must explain for the “naive” reader who won’t look at the reference. However, good job on explaining the choice of parameters!

### 2) TWI

OK!

### 3) Functional traits

- 1.210 is it plural (proxies)? If yes, be consistent throughout the study between “index” (plural) and “indices” (used later in your text). I personally find “indices” (or “indexes”) disambiguating. If no, change to “as a proxy”.
- 1.217 “using the mean **trait** values”
- 1.218 “of Vleminckx” → “that Vleminckx” or “the 120 species Vleminckx *et al.* (2021) and our study have in common / share”

## *Analyses*

The structure is very clear and helps following what you do.

However, I would expect you to refer to the questions at the end of your introduction. Not necessarily to present the analyses following the same order, but perhaps precisising which question you explore in each paragraph. Let me guess: first paragraph → question 3; second paragraph → question 1 (which makes me wonder if you should not precise in your question 1 “tropical tree **species**”); third paragraph → question 2.

### 1) Effect of phylogeny and environment on individual growth

- 1.225 effect of phylogeny and environment → on what? You say it right after but maybe repeat “on individual growth”.

### 2) Species growth potential across phylogeny

- 1.233 you did not describe the “log-normal distribution of individual growth potential within species”, can you provide a Supplementary or refer to another paper?
- 1.233 the median as opposed to the mean?
- I have no expertise on phylogeny and did not comment on the analyses you performed concerning it.

### 3) Link between functional traits and species growth potential

- 1.242 and 243 I do not mind, but some statisticians would want a justification on using log-transformed data (to ensure normality of residuals / to refer to a linear framework...).

## **Results**

I like that it follows the same structure than the analyses paragraph.

### 1)

- Refer to Fig. 1B for the taxonomic levels

- 1.256 “explains” → “explained”
- 1.259 and 261 Fig. 1A

2)

- 1.265 “phylogenetic autocorrelogram” → “phylogenetic autocorrelograms”?
- 1.265 and 270 Fig. 1C

3)

- 1.279 “6” → “six”

Table 1:

- Precise that “Residuals” is considered as variability “Among individuals within species” in your results paragraph (and not just some measurement error).

Figure 1:

- BEWARE, in the legend there are **missing formulas!**
- Panel B: could you use a colour-blind friendly palette (like viridis magma or plasma to differ from panels A and C)?
- Panel B: precise that you partition residual variance (you do not take into account the variation explained by fixed effects)
- Legend of B: needs to be re-written. Suggestion: “The variation of individual growth potential shows most of the variation **is explained** at the individual **level** then by genus before species and family.”
- You cite Fig. S2 but you comment Fig. S1

Table 2: OK (I like the presentation of your tables)

## **Discussion**

### *Introductory paragraph*

I like the quick results synthesis and the introduction of your main discussion themes.

- 1.324-326: you say that forest gap dynamics resulted in fast-growing vs. slow-growing strategies (by the way I would not say it results in fast/slow-growing *trees* but fast/slow-growing *strategies* within trees), but it seems like you are still synthesising your results while you already propose an explanation for this result, right? Make it obvious (could, might...). Or if you refer to the fact that NCI plays a role in growth in your study, precise that it is this observation that you connect to forest gap dynamics.
- 1.329: these hyperdiverse ecosystems: I know you are referring to tropical forests, but you did not precise this before and therefore “these” do not refer to anything. Maybe “individuals in hyperdiverse ecosystems like tropical forests”?

### *Evolutionary history shapes the growth of tropical trees*

- 1.350 individual variation in growth **that is** stronger than
- 1.353 “Several convergent evolution” can we say several evolutions (used 1.408)? If yes, then use plural. If not, maybe “convergent evolution events”.
- I wonder if you could finish this part opening on the next one rather than the last one. You could for instance say that as the species level seems relevant, understanding its functional

aspects seems to be a promising trail (as said by many functional ecologists before). You would then keep the transition to individual variability for the end of the next paragraph, though I think you have to keep the remarks of your current last sentence.

### *Multiple functional dimensions together predict the species growth potential*

- 1.382 “shown as a major predictor” → “shown to be a major predictor”?
- 1.398 beware of the format of the reference
- I confirm that a transition is lacking to hop to the next paragraph.
- 1.391: look up for instance Monique Weemstra (Miami), Kerstin Pierick (Göttingen), Guangqi Zhang (Montpellier), I do not promise they did show this in the tropics but there are currently many people working on adapting the root economic spectrum to the tropics.

### *Individual growth potential is influenced by forest gap dynamics but remains largely unexplained*

- 1.415 and 472: you never defined CVlog before.
- 1.421-422 replace “species” by “strategies” as you already precise that it’s at the interspecific level?
- 1.425 “niche successional-breadth” → “sucessional niche breadth”?
- 1.435 dynamics → result
- 1.437-439: To me it is a complicated sentence. You could cut the sentence rather than put “, and” and remove “within species”. I think the reader understands at this point that you are talking about individuals within species. I also wonder if you can say that you found that slow-growing vs. fast growing species/individuals were in early vs. late succession niches. That is an interpretation of the results with NCI rather than a result, isn’t it? Then I would precise “we found...and interpreted this as...”.
- 1.445 “The role of topography on individual growth potential was weak” is redundant with your previous sentences, you could go on with “We can however assume...”
- 1.450 remove “And”
- 1.451 “and other undetermined factors”?
- 1.451 “remains also” → “also remains”
- 1.457 “shapes” → “shape” (also you do not want to attach it to “could”)
- I commented the contents of the last paragraph earlier.
- 1.467 “supports” → “support”
- 1.469: I do not understand the link between the fact that late-succesional species have more variable responses to competition and light variation on the one hand and the closure of the canopy during succession on the other hand. Indeed, late-successional species thrive in the already closed canopy. If you mean that the closed canopy offers more diverse light-environments than an open canopy or a canopy that is starting to close, you should say it.

### *Supplementary materials*

- I highly recommend to **use PDF format** to ensure that each reader can have access to all elements in the document. For instance I could not see all equations in Table 1.
- In Table 2, add “effects” (e.g. “Individual fixed” → “Individual fixed effect”) or use abbreviations (FE and RE).
- In Figure S2, could you precise what are NA data? Maybe it is species that were not selected for the study? Or is it that there were not enough data to infer the indicator?
- Figure S3: 99 or 999 bootstraps like the previous correlogram? You do not report significance here although you comment it in the main text (1.281). Either do not comment significance or provide the corresponding material (I think it’s okay if it means many supplementary figures).

