(temporary section)

Nidhi, I like to use the following system for reviewer responses:

italics = comments/ notes/ tentative responses that still require work

bold= completed responses

For issues that require discussion, it's helpful to open an issue and link to it under the reviewer comment.

Dear Editor:

We are pleased to submit a revised version of our manuscript, "Thermal sensitivity across forest vertical profiles: patterns, mechanisms, and ecological implications" (NPH-TR-2021-38020), for consideration for publication in *New Phytologist*. We have addressed all points raised by the reviewers, as detailed below. The most significant changes include:

- …

- …

(To ensure rapid handling of your manuscript we would be grateful if you could confirm, in the cover letter to the Editor, whether or not there are any important elements of the figures that need to be retained (eg. colours used, plant species drawn, layout and spacing, symbols, etc) and if you have specific instructions that you would like the illustrator to take on board.)

Thank you for considering this revised version, and we look forward to your response.

Sincerely,

Nidhi Vinod & Kristina Anderson-Teixeira (on behalf of all coauthors)

Response to Reviewer(s)' Comments to Author:

Referee: 1

General comment:

The article is easy to read and well structured, I appreciated reading it. It covers a broad area and explains relatively complex ideas in simple terms and efficiently. I also enjoyed the changes in scale (leaf scale to ecosystem scale). I think this paper will be very useful as a reference for the plant physiologist community and for modelers.

Thank you.

I have been really interested in the comparison between gradients in canopy of individual trees and canopy made of an assemblage of species (paragraph 3.1 and 3.2. However, the paragraph 3.2 is relatively short, and I am curious if it can be developed a little bit more (maybe not!).

https://github.com/EcoClimLab/vertical-thermal-review/issues/99

I find it interesting to try and link the empirical and theoretical knowledge on vertical gradients in forests with what is done in DGCMs and what should be done to improve their accuracy. However, I think there is a big step between the review (part I and II) and the author's view on the implications for models (Scaling across space and time). I wonder if it would be possible to link a little bit more the different parts, and maybe without going that much in the technical details (cohort, big leaf, multi layers, …) which I think are sometimes imprecise or maybe wrong. Would it be possible to explain more simply what are the vertical gradients presented in the section II, that are misrepresented today in DGCMs? Maybe by explaining which of the 'biophysical variables' and 'leaf traits' that you listed, are considered constant when they should be variable vertically?

Thank you for the comment. We included a section that explains how vertical gradients are represented in models (see LXX-XX). Given that models vary greatly in how they capture vertical light gradients, what biophysical variables are included and how those variables are parameterized to vary (or not) across vertical gradients, we feel that it is beyond the scope of this paper to comprehensively list or explain which of those variables vary vertically across different models.

https://github.com/EcoClimLab/vertical-thermal-review/issues/82

Minor details that I hope will be of interest for the authors. Consider them as you see fit.

L30 I did not understand 'Scaling up' in this sentence.

Figure 1 is nice. I struggled with 'Tleaf sensitivity to shortwave radiation' but I think it is clear after, when reading the text. Consider using the same words in the paragraph where

you detail it (line 268?) and adding the reference to the figure in the text. Or maybe change the term ('thermal capacitance' ?) if this is the part you are referring to in the text.

Done

Figure 2: Homogenize the units (in parenthesis or in bracket) and add the unit for PAR.

issue #83

I like your figures, but maybe consider homogenizing a little bit the styles for the plots between figures 2 3 and 4.

L205-206 Maybe add some references. How many degrees? In your Figure 3 there is not really a difference between Tleaf and Tair when SWR = 0. Given that the transpiration nearly stops at night (high humidity, low conductance) I would expect Tleaf – Tair to be very close to zero.

Tleaf can be well below Tair on clear nights despite low transpiration, due to radiative coupling with the very cold sky. Added the following references to L205-206: Therefore, leaves are typically cooler than the air at night, and under some daytime conditions (cloudy skies, high wind speeds, and high T_{air})(Vogel, 2009; Rey-Sánchez *et al.*, 2016; Cavaleri, 2020)

Agree, but we're only changing the one variable at a time. Just need to make this clear.

Yes, night time conditions entail a shift in Tair, which in our case is constant

L219, repetition with L 216

Done

Figure 3: TLeaf and Tleaf.

Done

l258 under soil wet conditions?

We have reworded this sentence to read, "In contrast, under conditions conducive to stomatal opening, higher wind speeds and enable cooling in the upper canopy, whereas lower wind and in the understory allow much less evaporative cooling (Fig. 3b,d, Roberts *et al.*, 1990; Martin *et al.*, 1999; Leigh *et al.*, 2017; Song *et al.*, 2020)."

L298-299 Far red to red light: I think this could be developed here or somewhere else. You covered the vertical variation in light quantity inside the canopy, but you could also report the vertical change in light quality (light spectrum) as the leaves absorb preferentially some wavelengths but reflects or transmit others.

Added the following lines: Canopy foliage absorbs a large portion of PAR, and selectively filters incident light along the gradient, therefore altering the spectral characteristics of light received in the lower canopy layers. Along with decreasing PAR, this entails a decrease in red to far red ratio of light as it reaches the forest floor,

where understories are enriched in near infrared radiation and absorb light in wavelengths of 700-1000nm [de Castro 2000; Poorter *et al.* 2000]

L 322 consider homogenizing the photosynthetic capacity (AA) with the other notations in Table 2.

Done

Table 1: Unit for PAR absorptance (should be % I think)

Thank you. The units in the table are in % now.

Paragraphs 3.1 and 3.2: I thought that the comparison between intra species and interspecies gradients is very interesting. I wondered if there are more studies to expand it. One key article that I know is (Lloyd et al., 2010) which showed that within tree gradients and between tree gradients are similar for a lot of leaf traits in tropical forests. I think this is one of the reasons why DGCMs are relatively accurate even if the canopy description is quite simple. (The vertical gradients in photosynthetic parameters are scaled on Na gradients, which are the same intra and between species in this study).

L429 I am not fully sure if I understood this sentence, consider maybe developing the idea. Do you mean that the variation is higher in canopy made of multi species than on the canopy of single species? If so, I didn't understand the comparison with understory species.

yes, I think this sentence is confusing now that I am reading it again, need to work on this

L470 A thought: Stomatal conductance is highly correlated to photosynthetic capacity (Wong et al., 1979) so the gradients in conductance are expected to follow the gradients in photosynthetic capacity. The water use efficiency (gs/A) or the slope parameter of conductance models (Medlyn et al., 2011) could change vertically inside the profiles. I don't know if there are a lot of studies on the vertical variation of the water use efficiency or the slope parameter, but that could be something interesting to mention. See for example (Buckley, 2021).

We appreciate this comment, and have added mention of the fact that maximum gs increases with light in the canopy because it typically tracks photosynthetic capacity, per Wong et al 1979. There is a great deal of literature showing that the relative limitation of photosynthesis by stomata (gs/A, or intrinsic WUE) tends to be greater in the upper canopy, which results in lower intercellular CO2 and C isotope discrimination, as noted in the original ms (lines xxx).

I also think you could describe a little bit more the hydraulic constraints that increase with height. See for example (Koch et al., 2004). I think there are also other papers discussing the effect of height on water potential and stomatal conductance. You mention some aspects of it later, around L 636.

We have added mention of a few papers documenting the hydraulic constraints with height as they affect stomatal conductance (Yoder et al. 1994, Koch et al. 2004, Sillett et al. 2010).

L471, I think the word conductance is missing.

Done

L 513 Vcmax (c in subscript?)

Done

L 609 It is a detail, but you sometimes use the word 'canopy' to describe the top of the vegetation, and sometimes you precise 'top of canopy'. You also use canopy to describe all the vegetation from understory to the canopy, and you sometimes change definition from one sentence to another. Usually, it is easy to understand with the context of the sentence, but you might want to be consistent everywhere.

L 665 though

Done

More details on my thoughts for the 'Scaling across space and time' paragraph:

Most DGCMs represent a vertical variability in the main physiological parameters (Vcmax, Jmax, Rdark, Na). See for example (Krinner et al., 2005; Clark et al., 2011; Oleson et al., 2013). They all use some form of an exponential decrease in the photosynthetic parameters from the canopy to the ground. Since a lot of parameters and variables depend on Vcmax (for example A and therefore gs), this allows the representation of the vertical variation of a lot of leaf traits and variables. Big leaf models have this capability (see for example Krinner et al. 2005 that you cited, Appendix, or Clark et al. 2011). I think it is not clear in the way you wrote this paragraph, and it looks like 'big leaf' models do not represent any vertical variation at all. Note also that it is possible to use multi-layer models with or without considering shaded and sunlit leaves (See for example Clark et al. 2011).

Thank you for noting the need to clarify this point. We have added a passage at the end of the sentence that mentions big-leaf models to clarify that they do indeed account for assumed vertical profiles: "...to big-leaf models that reduce 3D vegetation structure across the entire biosphere into a single vegetation layer, <u>implicitly capturing vertical profiles in light, photosynthetic capacity and other features by assuming those profiles are exponential and thus can be integrated analytically…</u>" (added text underlined here). We also deleted the clause that occurred two sentences later, that had said about big-leaf models: "...which do not represent any vertical stratification…"

We also added a paragraph that more clearly describes the methods used for light competition that enables the type of variation in physiological traits that you described (e.g., Vcmax). See lines X-X.

issue #82

To me, an important remark is that most gradients in DGVMs are prescribed. More data would of course help to better understand and quantify the gradients, and to compare them with model representations (part 'Scaling in situ data with remote sensing' of your paper). But in the end, the mechanisms explaining those gradients are still not really known, in the sense that they can't be efficiently modeled prognostically. This is due to the multiple

sources of parameters variation that you highlighted (light environment, temperature, hydraulic, …). A lot of research is done using optimality frameworks to try and predict the photosynthetic and other vegetation traits based on environmental variables. See for example (Ali et al., 2016; Buckley, 2021). A question I have, is if including more precise cohorts as you suggest, would improve the accuracy of models given all the uncertainty in the parametrization of their traits.

[This is essentially impossible to answer without doing the research. Perhaps you could just acknowledge that the value of different modeling approaches is difficult to judge a priori.]

We agree that there is a recognition in the modeling community that we do need improved understanding of the mechanisms to better represent the level of vertical variation desired by some. We added a sentence in LXX-XX to acknowledge that. We also removed some of the language that emphasizes cohort based models as the only or best way to do this.

issue #82

Table S3: Including the words vertical or vertical gradient could have been useful.

I included below some more references, mostly in the tropics.

(Kitajima et al., 1997; Valladares et al., 1997, 2000; Thomas & Bazzaz, 1999; Carswell et al., 2000; Koch et al., 2004; Coste et al., 2005; Domingues et al., 2005; Lloyd et al., 2010; Van Goethem et al., 2014; Crous et al., 2020; Béland & Baldocchi, 2021)

Ali AA, Xu C, Rogers A, Fisher RA, Wullschleger SD, Massoud EC, Vrugt JA, Muss JD, McDowell NG, Fisher JB, et al. 2016. A global scale mechanistic model of photosynthetic capacity (LUNA V1.0). Geoscientific Model Development 9: 587–606.

Béland M, Baldocchi DD. 2021. Vertical structure heterogeneity in broadleaf forests: Effects on light interception and canopy photosynthesis. Agricultural and Forest Meteorology 307: 108525.

Buckley TN. 2021. Optimal carbon partitioning helps reconcile the apparent divergence between optimal and observed canopy profiles of photosynthetic capacity. New Phytologist 230: 2246–2260.

Carswell FE, Meir P, Wandelli EV, Bonates LCM, Kruijt B, Barbosa EM, Nobre AD, Grace J, Jarvis PG. 2000. Photosynthetic capacity in a central Amazonian rain forest. Tree Physiology 20: 179–186.

Clark DB, Mercado LM, Sitch S, Jones CD, Gedney N, Best MJ, Pryor M, Rooney GG, Essery RLH, Blyth E, et al. 2011. The Joint UK Land Environment Simulator (JULES), model description – Part 2: Carbon fluxes and vegetation dynamics. Geoscientific Model Development 4: 701–722.

Coste S, Roggy J-C, Imbert P, Born C, Bonal D, Dreyer E. 2005. Leaf photosynthetic traits of 14 tropical rain forest species in relation to leaf nitrogen concentration and shade tolerance. Tree physiology 25: 1127–1137.

Crous KY, Campany CE, Lopez Rodriguez RA, Cano FJ, Ellsworth DS. 2020. [In Press] Canopy position affects photosynthesis and anatomy in mature Eucalyptus trees in elevated CO2. Tree Physiology.

Domingues TF, Berry JA, Martinelli LA, Ometto JP, Ehleringer JR. 2005. Parameterization of canopy structure and leaf-level gas exchange for an eastern Amazonian tropical rain forest (Tapajos National Forest, Para, Brazil). Earth Interactions 9: 1–23.

Kitajima K, Mulkey SS, Wright SJ. 1997. Seasonal leaf phenotypes in the canopy of a tropical dry forest: photosynthetic characteristics and associated traits. Oecologia 109: 490–498.

Koch GW, Sillett SC, Jennings GM, Davis SD. 2004. The limits to tree height. Nature 428: 851–854.

Krinner G, Viovy N, Noblet-Ducoudré N de, Ogée J, Polcher J, Friedlingstein P, Ciais P, Sitch S, Prentice IC. 2005. A dynamic global vegetation model for studies of the coupled atmosphere-biosphere system. Global Biogeochemical Cycles 19.

Lloyd J, Patiño S, Paiva RQ, Nardoto GB, Quesada CA, Santos AJB, Baker TR, Brand WA, Hilke I, Gielmann H, et al. 2010. Optimisation of photosynthetic carbon gain and within-canopy gradients of associated foliar traits for Amazon forest trees. Biogeosciences 7: 1833–1859.

Medlyn BE, Duursma RA, Eamus D, Ellsworth DS, Prentice IC, Barton CVM, Crous KY, Angelis PD, Freeman M, Wingate L. 2011. Reconciling the optimal and empirical approaches to modelling stomatal conductance. Global Change Biology 17: 2134–2144.

Oleson K, Lawrence D, Bonan G, Drewniak B, Huang M, Koven C, Levis S, Li F, Riley W, Subin Z, et al. 2013. Technical description of version 4.5 of the Community Land Model (CLM). Boulder, Colorado, US: NCAR TECHNICAL NOTES.

Thomas SC, Bazzaz FA. 1999. Asymptotic height as a predictor of photosynthetic characteristics in Malaysian rain forest trees. Ecology 80: 1607–1622. Valladares F, Allen MT, Pearcy RW. 1997. Photosynthetic responses to dynamic light under field conditions in six tropical rainforest shrubs occuring along a light gradient. Oecologia 111: 505–514.

Valladares F, Wright SJ, Lasso E, Kitajima K, Pearcy RW. 2000. Plastic phenotypic response to light of 16 congeneric shrubs from a Panamanian rainforest. Ecology 81: 1925–1936.

Van Goethem D, Potters G, De Smedt S, Gu L, Samson R. 2014. Seasonal, diurnal and vertical variation in photosynthetic parameters in Phyllostachys humilis bamboo plants. Photosynthesis Research 120: 331–346.

Wong SC, Cowan IR, Farquhar GD. 1979. Stomatal conductance correlates with photosynthetic capacity. Nature 282: 424–426.

Referee: 2

A defining feature of forest canopies is their vertical variation in environment and morphology and physiology, originally described through the sun-shade leaf dichotomy or even earlier through vertical stratification diagrams as in Pearson (1971), dating further

back such as the classic work of P. W. Richards (1952). Such observations were carried through to the forest meteorology community by Monteith, Jarvis and others in the 1980s (Monteith & Unsworth 1990), and there are well-known patterns in micrometeorology through canopies and first-principle understanding of their meaning for energy balance within canopies. I read this review keenly interested in what these known aspects would mean for the interactions amongst leaf traits and sensitivity to temperature, tie them back to some empirical findings of more recent vintage, and possibly to gain some insights into canopy dieback phenomena during heat events or with climate warming. In the end, the latter weren't discussed but the authors are applauded for taking on such a huge topic. Fig. 1 is a useful entrée to the subject area.

Thank you for the review. We have added citations to the references mentioned here. We have also added some discussion of canopy dieback events(?)… details.

Nidhi, be sure to cite all the references listed here.

It would be good to add some discussion of canopy dieback events. (issue #93)

Given the depth of what is known about within-canopy micrometeorology, I would have thought taking this on in a review wouldn't be needed, or would be daunting and require too much detail to cover it all. As it is, I found the article launches into the empirical info too early in such an article. The article could be improved by going through the theory of how momentum and mass-transfers are attenuated through canopies and then show the empirical info from NEON in America. Overall there is too little on the theory end of things and too much 'case study' for this kind of article (see Monteith and Unsworth, and Gates to enhance the first-principle theory). As an aside, there need to be a number of improvements in Fig. 2, with lines made bolder and also height should be normalised to height relative to the top of the canopy given that trees were very different heights and meteorological masts went above the canopy to different degrees. Doing so would help make the authors' point about differences in the Figure as well as convergence in certain properties inside canopies rather than everything being on a different y-scale.

It would be good to bring in more theory. (issue #94)

Fig 2: issue #83)

Certainly, a discussion with a micrometeorologist or atmospheric scientist, if not already had, could improve the manuscript. Statements like l. 156: 'Wind speeds are also higher at the top of the canopy, owing to the buffering effect of the canopy' are an awkward read. Buffering? There could be much improvement by looking at it the other way: wind will blow as it does at the top of the canopy until encountering the plant canopy top as an aerodynamic drag element; then the additional leaf area entrains air movement and sweep-eject motion and eddies are attenuated through the canopy resulting in progressively lower windspeeds deeper into canopies. I don't know how buffering enters into this, or what the authors mean here.

issue #95. We appreciate these comments and have added a discussion of canopy transport from a more theoretical perspective (lines xxx-xxx), immediately after the paragraph about

canopy radiation profiles and before those on CO2, H2O and temperature profiles. We have also modified the subsequent paragraph about wind speeds to eliminate the use of the confusing term "buffering".

We had also used the word "buffering" in different context, where the intention was to describe how canopy attenuation (of radiation and wind) can reduce daily extremes of temperature in the lower canopy and understory. We have modified the text in those places to clarify. For example,

> *"Canopy foliage acts as the primary physical barrier between the atmosphere and the forest floor, buffering multiple aspects of the understory conditions <u>from large fluctuations in conditions above the canopy</u>"; (line xxx) (new text underlined)*

> *"Air temperature (T_{air}) often shows little variation across the vertical gradient, but under certain circumstances, <u>attenuation of radiation and vertical transport of sensible heat by the canopy can buffer the lower canopy and understory from large diurnal swings in air temperature</u> ~~it can be significantly buffered by forest canopies~~"; (line xxx)*

> *"Typically, <u>diurnal temperature range is smaller beneath dense canopies than above, resulting in</u> ~~, dense canopies buffer understories from high maximum~~ T_{air} ~~more than open canopies, i.e., dense canopy understories can have~~ cooler maximum daytime T_{air} and warmer nighttime minimum T_{air} than open canopy understories or nearby clearings."*
>
> *(line xxx)*

I was eager to see the part of the manuscript about photoprotection and also its relationship to heat damage. The opening sentence (l. 384) was obvious to the point of being painful to read. Of course photoprotection is higher in the upper canopy: radiation levels are higher! Can this first sentence get revised to increase information content? This is one of the more exciting topics of the review, yet is handled only in a cursory fashion. If the authors could manage a bit more discussion of this topic it would be useful – instead they move (in the same paragraph) to VOC emissions, something I view as a separate capability of some plants. This is also confused in Fig. 1 where VAZ and VOC are placed on the same line. I'd like to see a more complete discussion of photoprotection and heat dissipation by NPQ first, and a separate paragraph about VOC. Also, there is nothing about critical temperature until late in the manuscript even though the authors skirt the issue in their text about photoprotection. This kind of thermal sensitivity is different from gas exchange (the section where the text about Tcrit occurs, l. 530-555), and should have been discussed earlier in the manuscript.

issue #92. It is not necessarily obvious that mid- or lower-canopy leaves should have less photoprotection, given that they may experience nearly the same peak radiation loads, during sunflecks, as leaves in the upper canopy, despite generally having less capacity to dissipate light by photochemistry.

In the first part of Section 5.1, the authors conclude this paragraph stating the 'dominant role of vertical profiles in microclimate in shaping tree growth rates'. However, I believe the

text has confused the very large effect of light with other aspects of forest microclimate, and they very much need to clarify this. If they believe other aspects of microclimate apart from light are drivers, then I believe this would be a minority opinion in the forest biology community. If they wish to speculate about other microclimate factors that cannot be disentangled from light, I suggest that they clearly indicate their opinion and speculation. It is perhaps an area for future research to disentangle light microclimate from aspects of vertical microclimate.

We did not intend to argue that light was not the dominant factor, but the wording was misleading. This sentence has been revised to read, "This points to a dominant role of vertical profiles in the biophysical environment, particularly light (Fig. 2), in shaping tree growth rates within forests."

I am uncomfortable reading some of the major conclusions of the work here, such as speculation that large canopy trees are most vulnerable to warming when water is limited, but understory trees may be more vulnerable [to warming] when well-watered. This is not consistent with my knowledge of 'preponderance of available data'. Perhaps the authors implying that understory trees will succumb to warming earlier in a heat wave than large canopy trees? Is this based on the T50 evidence (l. 542-548) which is from 2 studies, or from one tree-ring study (l. 674-676), or both? An intriguing thought, but these studies and the corresponding author's study have weaknesses and no clean experiment on this has been set up and done. I recommend that the more cautious language on l. 676-678 should in fact be repeated in the conclusions relevant to this point. It's less stimulating and sober, but true, that it's difficult to say so with strength of evidence and remains for further testing with good experimental design. An objective of such a review can stimulate further and better research.

We agree that more caution is warranted on comparing canopy vs understory responses to warming, particularly because understory responses are highly uncertain. We have reworded relevant text as follows:

- **"Implications: Global Change Responses : Warming" section, 4th par (previous lines 793-797: "While it is currently difficult to predict whether canopy or understory photosynthesis is likely to be more severely affected by higher T_{air} (see section 4.2), *limited tree-ring evidence* indicates that understory trees *can* exhibit greater reductions in growth during unusually hot growing seasons (section 5.1, Fig 4b, Rollinson *et al.*, 2020)."**

- **"Implications: Global Change Responses : Warming" section, final par (previous lines 803-806: "We expect that the tallest trees will be increasingly prone to hydraulic failure and damaging or lethal T_{leaf}'s, *while much larger uncertainty remains surrounding the responses of understory trees*."**

- **Conclusions section, first part (text specifically cited in the comment above): "Similarly, much remains to be learned about how crown exposure influences the temperature sensitivity of woody stem growth. While the preponderance**

of available data suggest that large canopy trees are the most vulnerable to warming when water is limited, far less is known about the responses of understory trees, which might be more vulnerable to chronic warming stress under relatively mesic conditions (Fig. 4)."

Details

There are a few dense sentences or run-ons that could be revised. Lines 192-196 and lines 201-204, for instance. Please revise.

Done

line52: 'with decreases being more commonly documented across the world's forests'

line128: '… but understory leaf area density is often relatively high in the understory as well' sounds redundant. Please reword.

removed the second 'understory' word here: "Tropical and temperate forests with dense canopies dominated by broadleaf trees generally have highest leaf area density in the upper canopy layers, but understory leaf area density is often relatively high as well..".

line140 'Light … decreases from the canopy top to the forest floor' – why isn't foliage clumping mentioned here amongst the other factors?

Light, specifically the proportion of incident light and photosynthetically active radiation (PAR), decreases from the canopy top to the forest floor. The profile shape of light is modified by leaf area density, leaf clumping, canopy height, and canopy structure across species and forest types (Fig. 2a-d, Supporting Information Figure S1, Koike et al., 2001).

line148: 'Variability in the light environment decreases with height' – I don't see this except perhaps at z = 0 and even so seems tenuous. Explain.

Fig. 1: In the diagram, stomatal density, leaf angle are separate categories yet VAZ and VOC are not. As far as I know though, there is no biochemical link between VAZ and VOC, so these should be separate shouldn't they?

Done *Need to replace updated Fig 1 image in the .rmd once all changes are made*

Fig. 2 is a mix of computed and measured quantities. LAD and proportion of sun leaves are both computed quantities, and the basis of these should be clearer. Or at least state 'modelled LAD' and 'calculated proportion of sun leaves'.

Done

line165-172: refixation of respired CO_2 in the understory isn't mentioned here, but there have been a number of studies, particularly involving 13C, that have looked at this. Please mention along with at least 1 reference.

line185: Buffering again. I supposed what is 'buffering' for the authors would conventionally be thought of differently by meteorologists. Please consult with one of them, and consider using different wording.

This passage now occurs after the new paragraph about turbulent transport within canopies. We have reworded the passage as, "Despite the complexities of turbulent transport in canopies, wind speeds are generally much higher at the top of the canopy (Jiao-jun et al., 2004; Jucker et al., 2018)."

line187: Where mentioning radiation fluxes, could I please ask the authors to use the phrase 'and sensible heat emission'? I think this is really what the authors are referring to, so why not say so?

Done

line188: 'dense canopies buffer understories' is one perspective, that there is far less radiant energy received and therefore understories stay cool is another. Can the authors please consider reflecting this perspective? I've studies canopies for a a score of years and I just don't think 'buffering' is at play so much!

We were using the term "buffer" in a functional or biological sense, meaning "protect," rather than as a description of the underlying physics; i.e., the canopy protects the understory from large diel swings in both air temperature and radiation. We have reworded this passage to clarify: "Typically, <u>diel temperature range is smaller beneath dense canopies than above, resulting in</u> , dense canopies buffer understories from high maximum T_{air} more than open canopies, i.e., dense canopy understories can have cooler maximum daytime T_{air} and warmer nighttime minimum T_{air} than open canopy understories or nearby clearings."

line199 should end with something like 'to shape Tleaf patterns within canopies' rather than just drop at Tleaf.

Done

line206-207 'Leaves are typically warmer than air …'. That is not what is predicted in theory, proven by parts of the simulations in Fig. 3. Why not use 'Leaves can be warmer …'? That would be more consistent.

Done

Figure 3: Variables in the inset table need to be stated. I can guess what they are, but this should be explicit.

Figure 3: Humid and drought is not a straight comparison. Well-watered vs. drought would be clearer as there are some assumptions about gs in these conditions that underlie the modelling being done here.

We changed to "humid" to "moist" (as opposed to "well-watered"). We chose the term "moist" because it conveys both high soil moisture and atmospheric humidity, which is what we aim to capture.

Figure 3: why not put a point that represents the leaf values for top and bottom of the canopy?

https://github.com/EcoClimLab/vertical-thermal-review/issues/84

Table 1: What is here is not leaf gas exchange, and it seems that the authors have repeated the caption for Table 2 in error. Please fix this. Also don't capitalise 'leaf'.

Done *Need to add the updated table to .rmd*

Lines 354-372 on sun versus shade leaves and Table 1. Most of what is here was known a long time ago, say in Vogel 1968 (cited) and Boardman 1977 (not cited) but pertains to within-canopy rather than between sun and shade plants. I would suggest that this would be improved if the authors started from these old studies that most readers will recognise, and state how we've advanced in understanding and progressed toward within-canopy work rather than between sun-and-shade habitats.

line382: 'more frequent stomatal closure higher' is awkward and does not follow the comparative. Higher than what?

line383: d13C is NOT a concentration, it is an isotope ratio. Please revise.

Done

line404-405: A cause-effect for an earlier, juvenile understory tree leaf-out is implied here, and I;m not sure that is demonstrated. There are other phenomena underlying this e.g. turgor, hydraulics, hormones, etc.

Thank you for pointing this out. In line404-405, we are concentrated on interactions between microenvironments and function. We edited the text to emphasize the mechanisms for earlier bud break in the understory, including warmer temperatures, and the benefits of maximizing carbon gain before overstory closure reduces light availability (added ref. Lee & Ibáñez, 2021). We edited the rest of the paragraph to more clearly emphasize mechanisms of feedbacks between vertically structured microenvironments, leaf phenology, and forest function.

line475: 'because water supply often cannot meet the demands incurred …'. How do we know how frequent this is? Evidence?

We have added four references showing that stomatal conductance is often limited by imbalance of water supply and evaporative demand for leaves in more elevated or more sunlit canopy positions (Yoder et al 1994, Kock et al 2004, Sillett et al 2010, Buckley et al. 2014).

line478: 'intracellular CO_2' needs to be fixed.

Done

line479: 'In sun leaves, Tleaf thus further increases'. Further than what? Comparatives should have be clear what we're comparing to.

This sentence has been rewritten as, "Stomatal closure reduces transpirational cooling, thus amplifying the warming of sun leaves by high radiation loads."

line481 'is maximized' or is maximal? Please correct.

We have replaced "maximal" with "greatest".

line485-487: It seems that VPD and its effect on gs is ignored here. Please clarify? The well-known stomatal closure at high VPD alone would mean higher Tair would decrease gs in the upper canopy (not 'canopy leaves' as stated) compared to the lower canopy. See Grossiord et al. (2020) Tansley Review. VPD only gets mentioned in the section on photosynthesis (l. 496). Please do so earlier.

We agree, and have modified the text in this section to emphasize the role of VPD in driving stomatal closure in sun leaves (new text underlined): "However, ~~because~~ water supply often cannot meet the demands incurred by the high irradiance and g_b experienced by sun leaves <u>with fully open stomata, because of height-related constraints on water transport (e.g., Yoder et al. 1994, Koch et al. 2004, Sillett et al 2010) and/or because of increased evaporative demand (VPD) caused by leaf warming in sunlit canopy locations (Buckley et al. 2014). As a result,</u> midday stomatal depression is more prevalent in sun leaves than shade leaves in closed-canopy forests (Table 2), which drives the lower intracellular CO_2 and carbon isotope discrimination discussed in section 3.1 (Table 1). <u>Stomatal depression reduces transpirational cooling, thus amplifying the warming of sun leaves by high radiation loads</u> ~~In sun leaves, Tleaf thus further increases due to the lack of transpirational cooling.~~" We have also added the phrase "<u>(driven by increased VPD)</u>" after "sun leaves in the upper canopy show a stronger decrease in g_s in response to rising T_{air}", and clarified that "high T_{air} should decrease g_s of <u>upper</u> canopy leaves".

line510-525: There is a long discussion about whether Topt for gas exchange or its components differs between overstory and understory. Here the authors aren't clear, but such a comparison only matters if the same species is measured in different canopy layers.

The section on VOC emissions was interesting and informative.

Thank you.

line641: 'tends to be greater in canopy trees'. Greater than what? Please state the comparison.

This sentence has been revised to read, "In turn, the drought sensitivity of woody growth tends to be greater in canopy trees than in smaller trees with less exposed crowns."

line650: 'In addition to lower drought resistance of growth, larger trees frequently exhibit lower ability to recover'. Having studied large overstory trees and young understory

saplings, I have a very, very difficult time with this statement especially portraying it as categorically true even if consistent with the 4 cited studies. Very few researchers have studies the same species in this context, and in this review manuscript the authors cannot scientifically lay the effect on canopy position and microclimate rather than age or other confounding factors. I must challenge their assertion and ask a higher level of evidence to make these statements, which should be qualified.

As the point about resilience was not critical, we have removed that part of the statement. The sentence now reads, "In addition to lower drought resistance of growth, larger trees frequently exhibit greater increases in mortality (Bennett *et al.*, 2015; Stovall *et al.*, 2019)."

line946: '… how … temperature sensitivities of metabolism and woody growth vary across these vertical gradients'. I'm not sure why the authors are speculating on woody growth in this context, surely it would be extremely difficult to show that woody growth varied vertically in an individual? And that across-individual differences compound comparisons of individuals in different vertical strata? Shouldn't these things be pointed out to readers?

This has been reworded to read, "However, there remains a lot of uncertainty as to how temperature sensitivity of foliar gas exchange varies across these vertical gradients. Similarly, much remains to be learned about how crown exposure influences the temperature sensitivity of woody stem growth. While the preponderance of available data suggest that large canopy trees are the most vulnerable to warming when water is limited, far less is known about the responses of understory trees, which might be more vulnerable to chronic warming stress under relatively mesic conditions (Fig. 4)."

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