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 in our responses to the reviewers. The most significant change was de-emphasizing the discussion of the potential for stronger negative effects of rising temperatures on understory trees, including removal of former Fig. 4b and modifying the text throughout to give a more consistent message (as requested by reviewer #2).

Regarding production of the figures, below are some specific criteria:

* It will generally be fine to adjust colors, layout, and spacing on the figures.
* We would like to retain the background painting in Figure 1 (by the lead author)

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

Comments to the Author

I am satisfied with the corrections and the responses to the comments. I like the new structure, the writting is very precise while covering broad areas and the paper very interesting.

**Thank you.**

Some minor points :

-PAR units in Fig 2d

**Fixed.**

-Fig 3 caption: TLeaf and some other discreptances with rest of the paper abreviations or format (tair, gs)

**Fixed.**

-l304 Not sure about the structure of the sentence and causality. Gravity and hydraulic pathlength (due to height) could mitigate the effect of light alone ?

**The full sentence reads: “More recent work has extended the focus from light alone to *height* in the vertical profile, as *the latter* shapes differences in leaf structure and function that can partially mitigate the effects of gravity and hydraulic pathlength on leaves higher up in the canopy.” Thus, we’re saying that *height* shapes differences in leaf traits that could mitigate effects of gravity and hydraulic pathlength. We believe the sentence to be correct as written.**

-Table 2, gb unit, mmol m-2 s-1 ?

**Done**

-I found the x axes labels in Fig 4.a difficult to understand, there is maybe a more intuitive way to write them. Note that PET is not defined. °C for the units.

**We have fixed the axes labels to list units as °C and updated the caption to define PET and better explain the x-axis labels.**

## Referee: 2

Comments to the Author The authors seek to tackle a fairly complex topic in this review article. Whilst the topic of vertical variation in forest canopies is fairly specialised, they have pulled together quite a large body of literature and the review cuts across the fields of micrometeorology, physiology and ecology for forests, and many will want to read and perhaps cite the review.

**Thank you.**

The authors have done a good job of addressing the reviewers’ comments from my inspection. This reviewer apologises for needing to raise additional points that were not raised in the previous reviews of the article, but some conceptual aspects and some of the writing are perhaps flawed or require clarification. There are some additions done in the review process that have confused things, or a few aspects that were not picked up in the initial review. The authors and readers both benefit from a clearer picture emerging in this review. There are still a number of places where the authors could improve and one cannot resist letting these past at this point.

**Thank you for your additional comments.**

The words ‘disproportionate’ or ‘disproportionately’ are used l. 33, 35, 504, 648, 814, 838. For instance, l. 35 ‘disproportionately impacted under hot, humid conditions’: disproportionate to what? The implication is disproportionate to canopy trees, but there is almost no evidence of this. The authors need to be clear what the comparative is in each case that a form of ‘disproportionate’ is used, especially in their abstract.

**We have modified these statements as follows:**

**l.33 - “Scaling from leaves to trees, canopy trees have higher absolute metabolic capacity and growth, yet are more vulnerable to drought and damaging *Tleaf* than their smaller counterparts, particularly under climate change.”**

**l.35 - “In contrast, understory trees experience fewer extreme high *Tleaf*’s but have fewer cooling mechanisms and thus may be strongly impacted by warming under some conditions, particularly when exposed to a harsher microenvironment through canopy disturbance.”**

**l.504 - “Early leaf-out gives saplings and seedlings a window for high photosynthesis before they are shaded by canopy leaves– contributing the majority of annual carbon fixation for some seedlings – before canopy foliage and reduces light availability (Augspurger & Bartlett, 2003; Lee & Ibáñez, 2021).”**

**l.648 - “Among these, the best-studied process is aboveground woody growth, which consumes only a modest fraction of total photosynthate (~1/6 on the ecosystem level, Anderson-Teixeira *et al.*, 2021) but, is critically important to long-term forest dynamics and carbon cycling because woody tissues have a long residence time in the ecosystem (Russell *et al.*, 2014).”**

**l.814 - “Large trees are also the most vulnerable to other climate-related disturbances (e.g., wind, lighting, Gora & Esquivel-Muelbert, 2021) that are expected to intensify with climate change (IPCC, 2021), and they are also targeted by selective logging (Miller *et al.*, 2011).”**

**l.838 - “In the understory, warming reduces the abundance of less thermally-adapted plant species, causing thermophilization of the plant community (Duque *et al.*, 2015; Greiser *et al.*, 2019; Zellweger *et al.*, 2020).”**

In fact, the abstract reads like the authors cannot decide whether tall trees ‘… are disproportionately vulnerable to drought and damaging 𝑇𝑙𝑒𝑎𝑓’ (l. 33) or understory trees (l. 35). It cannot be both if one is comparing them. In this aspect the abstract comes off indecisive or unclear. This is an element in the review as well (see below).

**We modified this sentence to read, “In contrast, understory trees experience fewer extreme high *Tleaf*’s but have fewer cooling mechanisms and thus may be strongly impacted by warming under some conditions, particularly when exposed to a harsher microenvironment through canopy disturbance.”**

I have issue with the ecosystem level being mentioned in the Abstract. There was little true ‘ecosystem level’ assessment done in the manuscript, and most of the ‘ecosystem level’ inferences are based on these statements which are indirect:

l.744 ‘Because canopy trees dominate these fluxes (Fig. 5), their responses will strongly influence the whole-ecosystem response’

l.898 ‘disproportionate role of large trees in ecosystem dynamics’

So perhaps the authors can greatly soften their ecosystem level assessment. To their credit, and what truly should be emphasised, is the further research needed on ecosystem function (l. 757).

**We have reworded the abstract sentence to place less emphasis on ecosystems: “Using published research and new analyses, we evaluate how microclimate and leaf temperatures, traits, and gas exchange vary vertically in forests, shaping tree and ecosystem ecology.” This wording parallels the section headers in the main manuscript. While we agree that there is little information on how ecosystem function varies across vertical profiles, this was included within the scope of our review, and we dedicate a 450-word subsection (sec. 5.2) plus a figure to this theme.**

l.32 tall trees have higher absolute metabolic capacity and growth at both individual *and ecosystem levels* (please remove the text between the asterices).

**Done.**

I make a major point of revisions around this idea (l. 35-36) that ‘understory trees may be disproportionately impacted under hot, humid conditions’. What evidence is there? There is speculation about what might happen in sunflecks (l. 800-801) but little direct evidence, and there is Fig. 4b which is one study with smoothed results that are not convincing (see above). Yet this statement is contrary to statements made in the actual review, like l. 200-201 to the effect that upper canopy is warming with higher VPD than understory, l. 232 that there are higher leaf-air temperature difference in the upper canopy than understory, l. 275-276 that leaves in the upper canopy have higher leaf-air temperature difference and maximum temperatures than understory, also l. 775-776. If so many arguments have been made for a harsher environment and higher leaf temperatures in the upper canopy than understory, it comes off as illogical to reverse and conclude on the basis of Fig. 4b which is flimsy evidence that, as stated in the abstract l. 35-36: ‘understory trees may be disproportionately impacted under hot, humid conditions’. I would suggest that the authors clean up their contentions and not come off so contrary to their own evidence and logic. Certainly this titillating idea of understory tree damage is not to be highlighted in the abstract if so much evidence to the contrary is presented in the review. I would like to see direct observations of the impacts that they suggest for the understory, but in the absence of strong arguments the balance of the review would support upper canopy vulnerability rather than the understory. This is a major aspect for the authors to clarify.

**We have greatly de-emphasized the discussion of the potential for stronger negative effects of rising temperatures on understory trees, including the following:**

**(1) removed Fig. 4b (from Rollinson *et al.*, 2020);**

**(2) modified the abstract sentence to read, “In contrast, understory trees experience fewer extreme high *Tleaf*’s but have fewer cooling mechanisms and thus may be strongly impacted by warming under some conditions, particularly when exposed to a harsher microenvironment through canopy disturbance.”**

**(3) changed statement summarizing Rollinson *et al.* (2020) to a more generic statement: “Indeed, there are cases where tree-ring records show more negative or less positive -responses of understory trees compared to canopy dominants (Rollinson *et al.*, 2020; Anderson-Teixeira *et al.*, 2022).”**

**(4) changed the statement, “…and tree ring evidence (Fig. 4) suggest that understory trees may respond more negatively to hot, wet conditions.” to read “…and some tree ring evidence (Rollinson *et al.*, 2020; Anderson-Teixeira *et al.*, 2022) raise the possibility that understory trees may be at a relative disadvantage under hot, humid conditions.”**

**(5) revised discussion in the “Warming” section to read: “In contrast, understory leaves and trees are unlikely to face the same absolute extremes of *Tleaf*, and protection from thermal stress associated with high direct radiation might allow shaded layers to photosynthesize longer in the day (He *et al.*, 2018; Miller *et al.*, 2021). However, with *Tair* more frequently equaling or exceeding photosynthetic optima, occasional exposure to sunflecks coupled with lower capacity to dissipate excess heat may prove disadvantageous. While it is currently difficult to predict whether canopy or understory photosynthesis will be more severely affected by warming (section 4.2), limited tree-ring evidence indicates that unusually hot growing seasons can dramatically reduce the growth of understory trees (Rollinson *et al.*, 2020), and these small trees may be at higher risk of carbon starvation because they have lower NSC reserves (Niinemets, 2010). Thus, despite their buffered microclimate, it is possible that understory trees could be more adversely impacted by warming temperatures than their canopy counterparts under some conditions.”**

**(6) in the conclusions section, removed the statement “…[understory trees] might be more vulnerable to chronic warming stress under relatively mesic conditions (Rollinson *et al.*, 2020)”**

These are wording issues where the writing can improve:

l.187: ‘but the elevated CO2 quickly dissipates during the day such that differences are negligible for most of the day when photosynthesis is occurring’. Please specify ‘CO2 concentration differences’ where it says differences, to increase clarity.

**Revised as suggested.**

l.200 ‘upper canopy leaves have higher 𝑔𝑏 and associated potential for water and heat loss’ compared to what??? Please clarify.

**Done. The sentence now reads: “The implication is that upper canopy leaves have higher *gb* and associated potential for water and heat loss compared to understory leaves (sections 2, 4.1).”**

l.256: The statement “During drought (hot and dry, with higher-than-average solar radiation) …” is worded in a confusing manner. Meteorological ‘Drought’ is conventionally defined as a prolonged shortage in the supply of water to land or plants, but with no link made to temperature or cloudiness. It is fine if the authors associate drought with high temperatures and high radiation, but the parenthetical should emphasise this association, whereas it could be read to imply a one-for-one relationship which is incorrect.

I suggest revising as ‘associated with conditions that are hot …’.

**Revised as suggested.**

l.264-265 ‘their environment is less conducive to dissipating excess heat compared to upper-canopy leaves.’ What evidence? This is a logical argument and should either be backed with references or labelled as a logical outcome of the conditions they have stated.

**We added an explanation to l.264-265 with references:** **"Thus, while understory and within-canopy shade leaves can remain cooler under lower radiation, their environment is less conducive to dissipating excess heat compared to upper-canopy leaves, *because wind speeds and hence boundary layer conductance are generally smaller in the lower canopy (Roberts et al., 1990; Martin et al., 1999).***

l.269 How does lower VPD in the understory inhibit evaporative cooling, if VPD is the major driver for evaporation? I think I understand how this can be counter-intuitive, but the reasoning isn’t explained so it all becomes opaque to the reader. Please explain very briefly.

**Lower VPD inhibits evaporative cooling precisely because VPD is the major driver for evaporation: Transpiration rate generally increases as VPD increases, and decreases as VPD decreases. Therefore lower VPD will mean less transpiration and hence less evaporative cooling. Perhaps the word *‘inhibits’* confused the issue; we have replaced *‘inhibits’* with *‘reduces’*. We have also modified the sentence to read, *‘In addition to lower wind speeds, higher RH (lower VPD) in the understory and inner canopy also reduces evaporative cooling (because evaporation rate generally increases with VPD), thus increasing Tleaf – Tair …’.* (phrase “because evaporation rate generally increases with VPD” added)**

l.313 ‘information from adjacent mature leaves or apical meristems, including a “memory” of previous conditions in that location, …’. This was not in the previous version that I can see, and I don’t see the basis for inclusion of this statement. As well, use of the term ‘memory’ seems awkward if not entirely wrong (even reading between quotes). Please revise.

**Revised as suggested.**

l.579 ‘implies that high 𝑇𝑎𝑖𝑟 should decrease 𝑔𝑠 of upper canopy leaves more than understory leaves’. The authors here are ignoring what they’ve said previously, that high Tair is associated with high VPD (l. 199-200), and that VPD is conclusively a much stronger driver of gs than Tleaf (Leuning 1995, Grossiord). I think the sentence should be corrected and include VPD. I’m not yet aware of a good study that has decoupled VPD and Tleaf to prove that Tleaf intrinsically causes reduction in gs. So the authors cannot conclude this.

**We have removed the quoted sentence as it was redundant with that which had preceded it, but had confusingly couched the message of the preceding sentence as if it were a speculation rather than an empirical fact. The preceding sentence, which we have retained, read:** ***“…sun leaves in the upper canopy show a stronger decrease in* *gs* *in response to rising* *Tair* *(driven by increased VPD) than lower-canopy shade leaves (Hernández et al., 2020; Carter et al., 2021)”.*** **That is an empirical result. The fact that the effect of *Tair* on *gs* in that result is driven by VPD rather than somehow directly by *Tair* itself is indicated by the fact that increasing temperature itself apparently *opens* stomata, rather than closing them. This is also germane to the reviewer’s final comment about decoupling VPD and *Tleaf*. There are in fact six published studies that have decoupled VPD and *Tleaf* (Schulze *et al.*, 1974; Hall *et al.*, 1975; Hall & Kaufmann, 1975; Fredeen & Sage, 1999; Mott & Peak, 2010; Urban *et al.*, 2017), and they all suggest temperature per se causes an increase, not a reduction, in stomatal conductance. We have added the following sentence to the end of the paragraph to clarify this matter, citing three of the six studies due to limit on word count: “Available data also suggest that high Tair can directly drive stomatal opening, if vapor pressure is experimentally adjusted in tandem with Tair to keep VPD constant (Fredeen & Sage, 1999; Mott & Peak, 2010; Urban et al., 2017), though it appears that the negative effect of temperature on gs, mediated by VPD, generally overrides the positive effect of temperature per se in nature, causing gs to decline when the leaf warms.”**

l.629 ‘we currently lack mechanistic understanding of how and why the temperature sensitivity of respiration varies across the forest vertical profile’. Other than that it varies according to the prevailing temperature difference? I think the temperature difference between upper and lower canopy positions, the theme of this review, should be mentioned in regard to this.

**Thanks for suggesting. We included the following sentence:** **Overall, although the temperature difference between upper and lower canopy positions is important driver of respiration, we currently lack mechanistic understanding of how and why its temperature sensitivity varies across the forest vertical profile.**

l.806-807 ‘trees in the understory might be more negatively affected by chronic stress from warming 𝑇𝑎𝑖𝑟’. This is based on such very thin evidence, almost no evidence. Nor do I think that the authors are appropriately highlighting a lack of knowledge very well by their speculation (which is not based on data). They are inferring what would happen with climate warming on the basis of historical evidence, highly indirect in Fig. 4B which only shows modelled results, and when there are highly overlapping CI’s. I hardly find it a basis for a strong statement landing in the abstract, especially when it is contradicted by other statements throughout the review.

**We have revised the second half of the paragraph containing this statement as follows: “In contrast, understory leaves and trees are unlikely to face the same absolute extremes of *Tleaf*, and protection from thermal stress associated with high direct radiation might allow shaded layers to photosynthesize longer in the day (He *et al.*, 2018; Miller *et al.*, 2021). However, with *Tair* more frequently equaling or exceeding photosynthetic optima, occasional exposure to sunflecks coupled with lower capacity to dissipate excess heat may prove disadvantageous. While it is currently difficult to predict whether canopy or understory photosynthesis will be more severely affected by warming (section 4.2), limited tree-ring evidence indicates that unusually hot growing seasons can dramatically reduce the growth of understory trees (Rollinson *et al.*, 2020), and these small trees may be at higher risk of carbon starvation because they have lower NSC reserves (Niinemets, 2010). Thus, despite their buffered microclimate, it is possible that understory trees could be more adversely impacted by warming temperatures than their canopy counterparts under some conditions.”**

**We have modified the abstract sentence to read, “In contrast, understory trees experience fewer extreme high *Tleaf*’s but have fewer cooling mechanisms and thus may be strongly impacted by warming under some conditions, particularly when exposed to a harsher microenvironment through canopy disturbance.”**

## References

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