**Title:** Thermal sensitivity across forest vertical profiles: patterns, mechanisms, and ecological implications

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## Summary

*(currently too long for NewPhyt)*

Rising temperatures are expected to have profound effects on forests; however, it is not well understood how responses will vary across forest strata. Here, we synthesize evidence as to how environmental conditions and foliar traits vary across vertical gradients, shaping leaf temperatures, metabolism, and ultimately whole-tree growth and mortality. Strong vertical microclimatic gradients imply that canopy leaves are exposed to more solar radiation and higher evaporative demand than understory leaves. However, foliar traits relevant to shaping leaf temperature () and metabolism also vary strongly across height or light gradients. Resulting ’s generally track air temperature () and do not vary dramatically across the vertical gradient, except when hydraulic limitations impede evaporative cooling such that ’s of sun-exposed canopy leaves become significantly elevated above both and understory . Correspondingly, while leaf metabolism generally increases with height across the vertical gradient, differences in thermal sensitivity, optimal temperatures, and thermal damage thresholds are modest. The implications for tree performance are mixed: whereas thermal buffering may contribute to the disproportionate stress of larger trees during drought, emerging tree-ring evidence suggests that understory trees experience relatively greater stress from high . Additional research will be important for improving our spotty understanding of the thermal sensitivity of metabolism and tree growth across vertical forest gradients. In the meantime, our findings imply that while large canopy trees are the most vulnerable to warming when combined with drought, understory trees may be more vulnerable under more mesic conditions.

## Introduction

Globally, temperatures have risen # C since YEAR and are expected to rise an additional #-#C by YEAR (IPCC REF). There is also increasing severity and frequency of heat waves (Perkins *et al.*, 2012). This is expected to have profound effects on forest biodiversity and ecosystem function (REFS), and the resulting feedbacks to the climate system (e.g., decreased C storage, altered albedo and hydrology) will have a critical influence on the future of trajectory of climate change (Bonan, 2016, Bonan 2008). These changes, alongside climate change-driven disturbances such as drought, deforestation and fire, may contribute to increasing tree mortality in forests around the world (McDowell *et al.*, 2008; Allen *et al.*, 2015, Brienen et al. 2015).

**Rising temperatures are likely to have differential impacts on trees of different size and canopy position, in large part because small understory trees exist in a microenvironment that is substantially buffered by the more exposed canopy trees (Davis *et al.*, 2019; Zellweger *et al.*, 2019).**

Taller trees form canopies that maintain vertically-stratified forest ecosystems, and play a crucial role in regulating macro-microclimate. (Nakamura *et al.*, 2017; Ozanne *et al.*, 2003)  
With increase in temperatures globally, we’re seeing that larger trees suffer more during drought (Bennett *et al.*, 2015; Stovall *et al.*, 2019). Increasing mortality of large trees, sometimes coupled with reduced tree growth rates, is driving a global trend towards more disturbed forests with younger trees (McDowell et al.2020).

**The structure and microclimates of global forests are changing due to unprecedented disturbance rates.**

Temperate and tropical forest canopies are already or will be soon functioning beyond their optimal photosynthetic threshold (Mau *et al.*, 2018; Huang *et al.*, 2019). Loss of canopy cover as a result of increasing temperature and related forest disturbances (Senf *et al.*, 2018; Senf & Seidl, 2020) is associated with reductions in canopy structural complexity, and altered microclimates and surface energy balance components (Stark *et al.*, 2020; Zellweger *et al.*, 2020), this has been shown to increase understory temperatures which raises concern for understory species and forest biodiversity (Zellweger *et al.*, 2019; De Frenne *et al.*, 2013)

(Marielle–“Reductions in canopy cover can lead to non-linear threshold responses, causing dramatic shifts from one forest state to another (e.g., transition from forest to savanna-like vegetation in tropical forest regions through”savannization“), with energy balance impacts and implications for forest-atmosphere interactions (Stark et al. 2020)”.)

We’re seeing increasing evidence that this impacts ecosystems, with potential feedbacks to climate change, especially in protecting species acclimated to cooler [mean annual] temperatures (Zellweger *et al.*, 2020; Scheffers *et al.*, 2013; De Frenne *et al.*, 2013; Suggitt *et al.*, 2018)

With shifting forest dynamics, it is becoming more important than ever to understand thermal sensitivity along the vertical canopy profile, from the understory to the top of the canopy, this will provide crucial insights for how rising temperature affects forest ecology and biodiversity, energy balance, ecosystem function, and biosphere-atmosphere interactions [with additional feedbacks to forest structure and microclimates].

(Niinemets *et al.* (2004) highlights biophysical and photosynthetic gradient interactions along the vertical canopy profile, however our current knowledge of this topic is lacking.)

**However, we lack a systematic, up to date understanding of biophysical and biological patterns across this gradient, how these affect leaf-level processes, and in turn how it affects ecosystems (Fig. 1).**

**This review addresses the following questions:**

1. How does the biophysical environment vary with height in forests? (“What aspects of biophysical envt? Microclimate and vertical plant structure/phenology/etc (ok yes, see this in fig 1)”?–Elsa So change to micrometeorological environment? Not biological just physical in this question, right?
2. How do leaf traits vary with height (or between sun and shade leaves) in forests?(What types of leaf traits?-E.O)
3. How do vertical changes in biophysical environment conditions and leaf traits combine to affect leaf temperature [and in turn photosynthetic capacity]??
4. How does leaf metabolism respond to temperature in canopy and understory settings?
5. What are the implications of these patterns for the ecology ecosystem and climate change responses of canopy versus understory trees?
6. What are the implications for modeling/ scaling / What are the implications of these leaf-scale responses at the ecosystem scale [in the context of climate change] / How do these leaf-level responses scale to entire ecosystems(*nerge these better*)

*Our primary interest is the gradient in height and exposure from the top of the canopy to the understory in forests. However, because a lot of the relevant research has focused on exposure gradients near ground level (e.g., comparisons of sun and shade leaves), and the implications [or utility] for ecosystem models we also review studies focused on exposure gradients.*



**Figure 1. (schematic of a forest summarizing most important gradients–sort of a “graphical abstract”.** Current version is just a very rough sketch of how this might look – needs to be filled in with content from the review. We could have a set of arrows for each of the major categories considered here. This would be a key figure, and should be beautifully illustrated—KAT could do a watercolor, or Nidhi could illustrate- and make use of NewPhyt’s figure editing service for Tansley reviews).

## The biophysical environment

The biophysical environment, here defined to include the physical structure of the forest canopy (from understory to the canopy top) and associated microclimates, is in large part determined by the structure of the forest itself. Canopy foliage, which varies across forest types and seasonally, strongly shapes the understory light, wind, etc. Forest canopies have a buffering effect on multiple aspects of the understory climate (Fig. **2**).

* (*Bonan (2016) reviews this and points to appropriate references*)

*(paragraph on leaf area distribution, including figure (*[*separate from or combined with current Fig. 2- see GitHub issue #15*](https://github.com/EcoClimLab/vertical-thermal-review/issues/15)*)* The vertical structure and hence, microenvironments of forest canopies vary seasonally (Parker & Tibbs 2004; Smith et al. 2019 ; Parker et al. 2019) and following disturbance (e.g., Parker et al. 2002 ; Almeida et al. 2016 ; Stark et al. 2020 in press). In this review, we focus primarily on growing season conditions, including leaf phenology at the edges of the growing season but excluding periods (in deciduous forests) when no leaves are present.

Light conditions, specifically photosynthetically active radiation (PAR) strongly varies with canopy height due to cumulative layers of vegetation that limits light to lower canopy layers (Niinemets & Anten, 2009; Fauset *et al.*, 2018; Parker 1995; Poorter *et al.*, 2019) (Fig. **2x**), such that the forest floor of understory regions receive 1-2% of the light incident to the top of the canopy [Roberts *et al.* (1990); Chazdon & Fetcher 1984; Parker et al. 2019]. In heterogeneous canopies [with high gap fractions], distance from the outer canopy is a better proxy for light environment than height (Parker 1995) and lower canopy light environments are highly variable, ranging from high light gap to deeply shaded understory regions (Chazdon & Fetcher, 1984; Smith *et al.*, 2019; Tymen *et al.*, 2017). This difference in light regime is an important variable in determining leaf traits along the gradient and consequently their responses to temperature (**???**; **???**; Doughty & Goulden, 2008). - Sunflecks: Leaky et al. 2003–from Marielle, “This is another, higher resolution axis of the variability of microenvironments that is probably quite important to address. (Also see the papers by Robin Chazdon on temporal variability of light environments). Maybe we will want to add these sentences (above) and something about sunflecks to a separate section that specifically addresses sources of variation in forest structure & microenvironments (e.g., vertical, horizontal, seasonal, diurnal, and with disturbance)?”

**Wind speeds are also higher at the top of the canopy (Fig.** 2x**).** *(fill in some specifics from the NEON analysis)* Consistent with the results from NEON sites, higher wind speed at greater heights within a forest have previously been observed in both closed canopy forests (e.g., REFS; McGregor *et al.*) and open savannas (Curtis et al. 2018). This results in higher boundary layer conductance () for canopy leaves. Boundary layer conductance is the thickness of air layer at the surface of the leaf through which water vapor diffuses after leaving the stomata;() also depends on leaf traits, morphology and windspeed. Large to heat transfer results in smaller difference in and (Roberts *et al.*, 1990; Martin *et al.*, 1999) thus having important implications for leaf thermal sensitivity.

**Air temperature, , is sometimes significantly buffered by forest canopies (Fig.** 2x**).** Studies comparing under forest canopies with nearby clearings have found lower maximum temperatures under forest canopies across Europe (**???**; Zellweger *et al.*, 2019) and in the northwestern United States (Davis *et al.*, 2019). Similarly, maximum air temperatures were higher above than below tropical forest canopies during wet seasons in Panama (Rey-Sánchez *et al.*, 2016) and coastal Brazil (Fauset *et al.*, 2018, Tymen et al. 2017). “max temps were higher and humidity lower in gaps vs understory regions (both at 1.5 m above the ground), see Fig. 4 - again illustrating buffering effect of the canopy”. However, similar maximum temperatures have been observed during the dry season in Panama (Rey-Sánchez *et al.*, 2016) and in a temperate deciduous forest in the eastern United States (McGregor *et al.*). Minimum is also buffered by forest canopies under some conditions. Higher minimum temperatures under forest canopies relative to nearby clearings have been observed across Europe (Zellweger *et al.*, 2019) and in the northwestern United States (Davis *et al.*, 2019). However, similar minimum temperatures under forest canopies have been observed in tropical forests in Panama (Rey-Sánchez *et al.*, 2016) and coastal Brazil (Fauset *et al.*, 2018), as well as in a temperate deciduous forest in the eastern United States (Nakamura *et al.*, 2017; McGregor *et al.*). *(Add something about risk of freeze.)* Additionally, canopies also buffer effects of snow through intercepting heavy snow accumulution on below-canopy levels (Storck *et al.*, 2002; Nakamura *et al.*, 2017)

**Humidity also varies across the forest vertical profile, being generally higher in the understory (Fig.** 2x**).** - DETAILS - REFS - McGregor *et al.*

Forest canopies moderate relative humidity in below-canopy microclimates along with temperature. In three European forest types (Broadleaved, Non-Pine Conifer, Pine) canopy buffering was observed to decrease daily maximum and increase daily minimum RH in below-canopy microclimate. With rising temperatures, this trend in maximum and RH would have implications on understory seedling growth, especially in high altitude temperate pine forests (**???**)

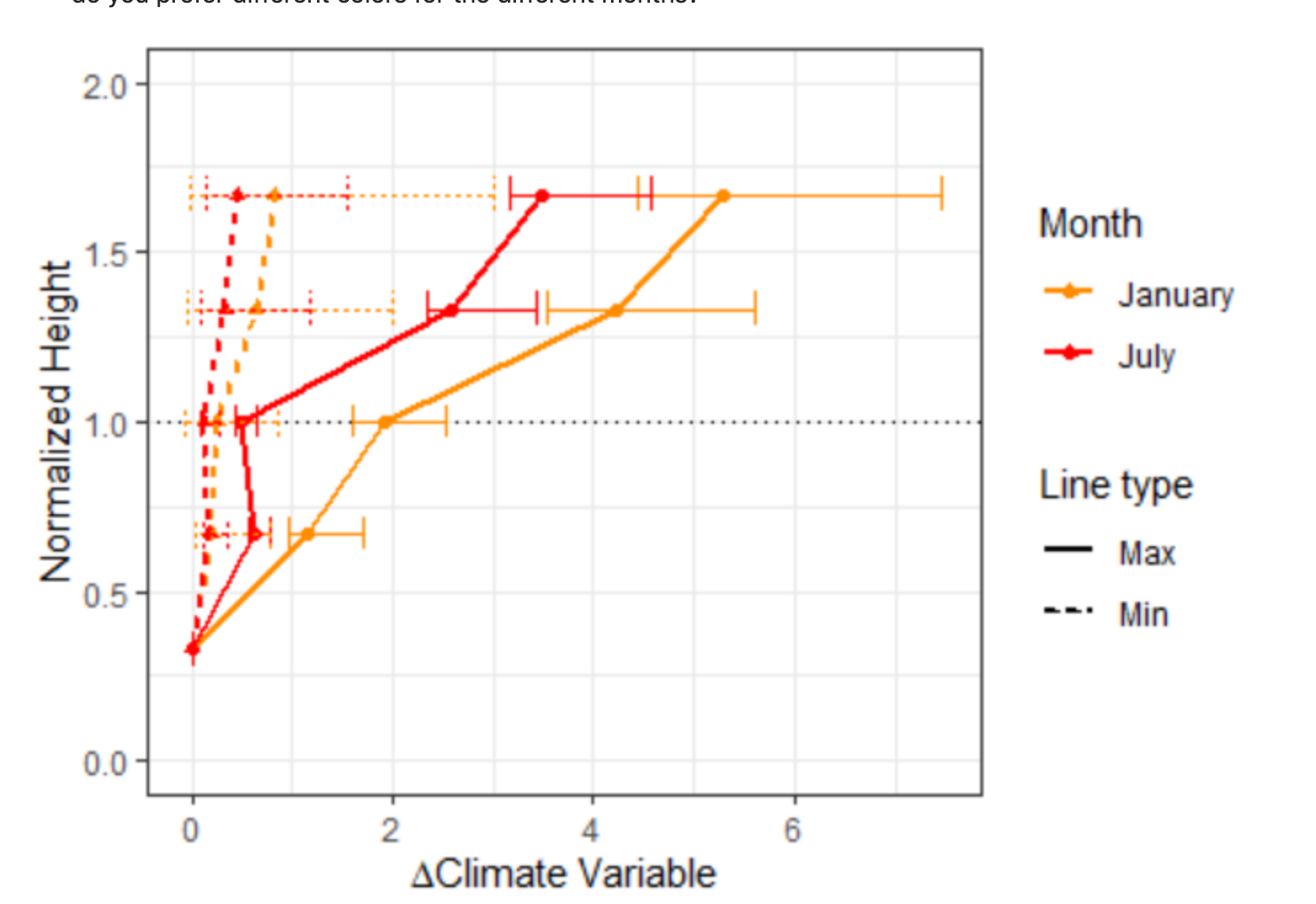
RH, in combination with temperature, determines vapor pressure deficit, - is lower in understory of Atlantic forest during wet season (Fauset *et al.*, 2018; Tymen *et al.*, 2017) This means that canopy leaves tend to be exposed to higher *evaporative demand*, higher stomtal contrains and lower osmotic potential, making canopy leaves more efficient in regulating water use (Niinemets & Valladares, 2004)

**Finally, carbon dioxide (CO2) concentrations tend to be higher in the understory.** - Higher in understory, particularly at dusk (Koike et al. 2001). - Higher in the understory overnight; difference persists during the day but is very small (Yang *et al.*, 1999). - Differences in concentration are by far most pronounced near ground level, as well, concentrations of (CO2) mole fraction values have been observed to be higher in lower canopy leaves compared with upper canopy leaves (Niinemets & Valladares, 2004)

Given that differences are small during the day when photosynthesis is active, and that even nighttime differences are modest at the height of understory tree crowns, CO2 concentration is unlikely to have much effect on the energy balance and metabolism of leaves across the forest vertical gradient.



**Figure 2. Vertical gradients in the biophysical environment, from NEON data.** Current placeholder figure is old version from Ian McGregor’s in press paper, showing NEON data from SCBI. See issue 2: <https://github.com/EcoClimLab/vertical-thermal-review/issues/2>.



This is a draft illustration of contents for the intendend figure. We’ll pick out one variable-month combination per panel, and show it for all the forested NEON sites.

**The strength of this buffering varies across forests, being influenced by both forest characteristics and the biophysical environment.** First, buffering increases with canopy cover. \* greater cover –> lower max T and VPD, higher minT (Davis *et al.*, 2019) \* greater cover –> lower max T and light availability (Zellweger *et al.*, 2019) \* [Thom *et al.* (2020); Tymen et al. 2017 ; Jucker et al. 2018 ; Hardwick et al. 2015] *Presumably, buffering would also be affected by canopy roughness, which affects turbulent air flow and the canopy boundary layer.* Taller trees don’t necessarily increase buffering (Zellweger *et al.*, 2019). Species that have higher shade casting ability such as braodleaved trees increase T buffering (Zellweger *et al.*, 2019, p. @vonarxSpatiotemporalEffectsForest2012) The strength of buffering also varies with respect to geographic and climatic factors. \* Distance to coast, topographic position, elevation (Zellweger *et al.*, 2019) \* (Davis *et al.*, 2019) However vertical climate gradients within forests are known to be steeper than those driven by elevation and latitude (Nakamura *et al.*, 2017; Martin *et al.*, 2020)

## Trait variation

Leaf traits vary along the vertical canopy profile following the pattern of light availability across the gradient (Poorter *et al.*, 2019). Leaves in the upper canopy that are exposed to more light differ in their traits compared to shaded leaves exposed to less light (Niinemets *et al.*, 2015). Increasing number of studies point towards the importance of incorporating vertical canopy leaf trait variation in modelling for leaf economic spectrum (LES) [Chen et al. 2020], leaf thermoregulation and thermal sensitivty which will provide a more accurate representation of within-canopy gradient response to increasing temperatures.[Fauset *et al.* (2018); Michaletz *et al.* (2016); Niinemets *et al.* (2015), Chen *et al.* (2020), REFS)

[Add something about how leaf traits along the vertical canopy profile are different than the expectation from leaf economic spectrum (LES)? Chen et al. 2020 is a good paper to help frame this . They make an important point in that paper that we may also want to make here: that the LES was ‘built’ using mainly sun (upper canopy) leaves; given the vastly different light environments at the bottom of the canopy (and that most leaves in the canopy are likely to be shade leaves) there is a strong research need to better characterise trait relationships and leaf responses through the whole vertical canopy - hence the importance of this review. Keenan & Niinemets 2016 will also be helpful in making this point.]–M N. Smith

**Many traits vary with height and/or between sun and shade leaves on the same species (Table 1).** Here, we focus on traits that are important for shaping leaf temperature () and thermal sensitivity.



(*For latest version of table, see tables.pdf.*)

Are traits shaped more by height or light? - “Height is more important than light in determining leaf morphology in a tropical forest” (Cavaleri et al. 2010) - (Cavaleri et al. 2008) - from Martijn: “If I remember correctly, height and light exposure are closely correlated and things like LMA scale with both, but above a certain level of light exposure, the effect of additional light disappears, while the relationship of the morphological traits with height continues. I have often been a bit skeptical about assuming height drives morphology, as most of the work that convincingly shows that (and relates it to turgor pressure for example) is from 100 m tall redwoods.”

*Leaf area / characteristic dimension*: - Recent paper on influence on leaf size/shape in PCE – certain aspects of leaf shape were not as relevant as expected. - Max stomatal conductance - increases with canopy height (Kenzo et al. 2015) Max transpiration rate - increases with canopy height (Kenzo et al. 2015).

*Thermal time constant (probably not a lot out there)* - Curtis et. al, 2018 – higher in more exposed leaves (heat up slower, cool slower) - Michaeletz has used this in theoretical calculations (Michaeletz et al. 2016 and 2015?

*Carotinoids/Xanthophyll cycle pigments* - photoprotective- disseminate heat, acclimate to high T. THese are proportional to irradiance - antioxidant scavenging function- protect against cellular damage - Koniger et. al. 1995, and Matsubara et al. 2009

*Isoprene production* - Isoprene production *capability* as a trait (actual isoprene production is in section 4. I’m not sure whether Ty’s content belongs here or in that section)

*(Paragraph on intra- vs inter-specific variation)*

* *Are patterns (in traits, metabolism, ecology) driven by tree height or exposure?*

## Leaf temperature and hydraulics

**Many of the biophysical and trait variable reviewed above affect leaf temperature, , which in turn has a strong influence on leaf metabolism (see following section).** is determined by the energy balance of a leaf and can be estimated based on basic biophysical principles (Campbell & Norman, 1998; Muir, 2019) (Fig. 3). While small leaves remain within a few degrees of , regardless of stomatal conductance, wider leaves can have temperatures deviating more from air temperature.(Fauset *et al.*, 2018) Large leaves can be significantly cooler than under low radiation with stomata open, and significantly hotter under high radiation with stomata closed.  
Leaves with open stomata and high radiation loads maintain similar to , with coolest leaves at intermediate sizes (~10mm). Shaded understory leaves should tend to maintain cooler daytime leaf temperatures for any given level of stomatal conductance. However, counteracting this, lower wind speed in understory would reduce latent heat loss. Thus, under hot conditions, canopy leaves exposed to higher wind speeds would be most effective at cooling when sufficient water is available to maintain high stomatal conductance; however, their can be highly elevated above when stomatal conductance is limiting.



**Figure 3. Leaf temperature in response to (a) XXX, (b) XXX (key trait or environmental variables).** Examples to be produced based on energy balance model using the tealeaves R package of Muir (2019): <https://github.com/EcoClimLab/vertical-thermal-review/issues/6>. Current placeholder shows figures from Campbell&Norman.

**Aligning with biophysical expectations, field observations have shown that leaf temperatures are influenced by the biophysical environment and leaf traits.** 1. Air T 2. Solar radiation 3. Leaf traits - Michaletz et al have done some interesting work on leaf thermoregulation in relation to various leaf traits. I don’t think there is sun vs shade tests, but we could look at how this might translate, or how some of the traits he has calculated might differ between sun and shade leaves. For example, he has this thermal time constant parameter that is calculated from leaf mass per area, leaf dry matter content, and some environmental parameters. E.g.: DOI: 10.1038/nplants.2016.129, <http://dx.doi.org/10.1016/j.tree.2015.09.006>

**When vertical gradients in the biophysical environment and leaf traits combine to shape leaf energy budgets, often differs little from and between understory and canopy (Fig.** 2?**).** For instance… (Bolstad et al. 1999). Similarly, during the dry season in a tropical moist forest in Panama… (Rey-Sánchez et al. 2016). **However, canopy leaves can reach much higher maximum , and higher , than understory leaves.** - (Slot et al. 2019) and refs therein - (Fauset et al. 2018) Sun leaves can also be cooled relative to more than shade leaves (Rey-Sánchez et al. 2016).

*(Because hydraulics are key to leaf T, we should include some of that here–e.g., water on leaves and leaf water content)*

## Leaf metabolism and thermal responses

Leaf metabolism is strongly shaped by leaf temperature, and by the traits and environmental drivers reviewed above, all of which vary across vertical forest gradients (Fig. 1). However, as we detail below, there are limited studies comparing thermal responses of sun and shade leaves (Table 2).



(*For latest version of table, see tables.pdf.*)

*Stomatal conductance*

*Photosynthesis*

**Photosynthesis is generally higher in sun leaves– a fact that is well-established (Niinemets 2007 ; Kenzo et al. 2015 ; Slot et al. 2019; Chen et al. 2020) and observed in numerous field studies.** This is primarily driven by the greater light available to sun leaves. In response to the greater light availability, sun leaves have traits allowing greater photosynthetic rates at high light, including …. The vertical gradient in photosythetic rates is also influenced by… .[thoughts: plasticity vs change in tree species composition through the canopy; differences in variability of microenvironments through the profile - highest lower down in canopy?; life history / investment strategies and hence, leaf life spans at leaves at the top vs bottom of the canopy]– M N. Smith

Photosynthesis increases with increasing temperature and irradiance, and saturates at quatum flux density of 400 to 700nm , beyond this the leaf experiences heat stress; non-photochemical quenching, photoinhibition and leaf necrosis. Leaves in upper canopy tend to experience more heat stress and greater photoinhibition than lower canopy leaves in conditions of water stress or drought. (Niinemets *et al.*, 2015)

**While sun and shade leaves differ dramatically in , the temperature sensitivity of photosynthesis does not appear to differ substantially between sun and shade leaves** Biophysically, we might expect that sun leaves should tend to have a stronger temperature-dependence and higher temperature optima than shade leaves (Fig. 14.5; *revisit this!*) (Campbell and Norman 1998) as observed by earlier studies, suggesting that the interaction between light gradient and temperature response along vertical canopy profile implied there to be a spectrum of temperature responses of , and along the gradient [Niinemets *et al.* (2004); Harley and Baldocchi 1995, Friend, 2001]. However, this does not appear to be the case based on the limited number of field studies that have compared temperature sensitivity of photoshythesis in sun and shade leaves. For 3 species in Panama, (**???**) found that the optimum temperature for sun leaves tended to be slightly higher than that of shade leaves, but differences were not significant. Similiar results were found for and (**???**, Hernandez et al.2020) Mau et al. found no trend along a height gradient in Puerto Rico, and no significant trend in temperate trees (Mau *et al.*, 2018).

**Leaf thermal tolerance (Tcrit/ T50)** - define. Typical values ~45-50C, varying somewhat across latitude/climate (O’sullivan et al. 2017), with elevation [Feeley *et al.* (2020); Slot unpublished data], with leaf traits (Sastry et al. 2018, Zhang *et al.*, 2012).

**Thermal tolerance (e.g., ) varies with exposure, but there are no studies isolating effect of height.** For two of three species studied in a tropical moist forest in Panama, was slightly lower for shade than sun-exposed leaves, both measured near ground level (Slot et al. 2019). Similarly, for *Acacia Papyrocarpa* (Benth.) trees in an arid region of southern Australia, higher was observed in more exposed (North-facing) canopy positions (Curtis et al. 2019). We’re not aware of any other studies on this.

*Respiration*

**Similar to photosynthesis, respiration tends to be higher in sun leaves (Chen et al. 2020), but its temperature sensitivity appears to be similar between between sun and shade leaves.** (Bolstad et al. 1999) did a study at Coweeta, including elev gradient. Found higher respiration (at reference T) in canopy leaves (Bolstad *et al.* (1999)). (*Martijn has some unpublished data on this that we might include:* [*https://github.com/EcoClimLab/vertical-thermal-review/issues/8*](https://github.com/EcoClimLab/vertical-thermal-review/issues/8)*.*) At Coweeta, Q10 showed a variable pattern, with a slight tendency to increase down the canopy (Bolstad *et al.*, 1999). (*Martijn has some unpublished data on this that we might include.unpublished data showing higher Q10 in shade than in sun leaves for 10 species or so. May make sense to include here:* [*https://github.com/EcoClimLab/vertical-thermal-review/issues/8*](https://github.com/EcoClimLab/vertical-thermal-review/issues/8)*.*) Combining reference respiration and , Bolstad *et al.* (1999) found a modest net decrease in R for understory leaves relative to canopy leaves as T increases (*see their Fig. 1*). Thus, Bolstad *et al.* (1999) found evidence of acclimation, but there remained a declining trend of respiration with elevation.

*VOC production*

**Isoprene production** - high emission rates occur in the mid-canopy, and even from very small statured trees and shrubs, at a site in the Brazilian Amazon (Taylor et al., in prep). - The high temperature carbon compensation point of sun leaves is higher in isoprene emitting species than in non-emitting species, so it is to be expected that other aspects of heat tolerance will be similarly affected by isoprenes (<https://doi.org/10.1111/pce.13564>). - Within species, isporene production scales with light/ T

## Ecosystem Scaling & implications

### Distribution of species and traits across the vertical profile

\*(This section should address inter-specific vs intra-specific variation, as Tables 1 and 2 refer to intra-specific variation, but most models will focus on trait variation across strata, regardless of species).

**Differences across forest vertical gradients in biophysical conditions, plant traits, and metabolism and its thermal responses scale up to affect whole-tree ecology in several ways.** First, vertical gradients in the biophysical environment shape which plant strategies, or sets of traits, are competitive in understory versus canopy conditions. - *Spring and fall leaf phenology in temperate deciduous forests (Augsburger). Mechanism: more moderate conditions (T, wind) in understory (REF).* *Among species that can be deciduous, greater proportion of deciduous individuals in larger size classes (Condit et al. 2000). One potential mechanism is lower temperature/hydraulic stress in understory* - something on isoprene production?

**Appears to affect community change under warming (Zellweger et al. 2020).**

### Scaling to tree level: demography

**Vertical gradients also affect tree growth and survival, and how these respond to climatic variation.** There are numerous demographic differences between understory and canopy trees, which have been linked to both the physical environment and plant traits (e.g., REFS), and we will not attempt to review those here. More interesting in this context is how these shape differences in the climatic sensitivity of growth and mortality. Many observations of larger trees suffering more during drought (Bennett et al. 2015). One likely mechanism behind this pattern is that the crowns of larger trees exist higher in the vertical profile and therefore are exposed to higher evaporative demand and solar radiation (McGregor *et al.*). Although drought is primarily a hydraulic problem, lack of water –> lower gs –> higher leaf T, so leaves face tradeoffs of water loss vs potentially damaging leafT.

**There is also recently emerging evidence that understory trees tend to exhibit greater growth declines with under mesic conditions.** In eight forests across the northeast United States, growth rates of understory trees declined sharply at higher (Rollinson et al., in review). Similarly, our previously unpublished analysis shows that in a broadleaf deciduous forest in Virginia, understory trees in a Mid-Atlantic forest responded more negatively to warmer than did canopy trees (Fig. **4**; Appendix **S3**). This pattern is initially counter-intuitive in that sun-exposed leaves can experience greater elevation of over than shade leaves (Fig. **3?**). However, given adequate moisture to sustain high , canopy leaves exposed to more wind and lower humidity should be more effective at cooling when exceeds physiological optima (Fig. **3**). It is also possible that competition is accelerated under warmer temperatures.



**Figure 4. Temperature sensitivity of tree growth (derived from tree rings) for understory versus canopy trees.** THIS IS A ROUGH PLACEHOLDER– KAT WILL PLAY WITH POTENTIAL VERSIONS. IF OUR IN-PREP TREE RING ANALYSIS METHODS PAPER IS ACCEPTED AHEAD OF THIS, WE CAN HIGHLIGHT RESULTS FROM THAT, WHICH ARE MORE RELIABLE. Analysis methods described in Appendix S3. OUTLIER HERE IS SHADE-TOLERANT BEECH. Data from Helcoski et al. 2019.

## Implications for Modeling / Scaling / Future Climate Projections

Elsa–The content below could probably be integrated in the above [Ecosystem Scale Implications] section, with subsections focusing on: - Suggested implications at the ecosystem scale based on literature - How do models currently integrate or not integrate these concepts and dynamics - What major gaps in knowledge and/or important questions emerge from this review (i.e. a lot of focus on droughts justifiably, but understanding heterogeneous impacts of temperature increases on forest ecosystems, particularly at vertically resolved scales is also important.) - What does that mean for about ability to predict/understand how forest ecosystems will respond in the future?

E.g. see de Pury & Farquhar, 1997 : though likely an improvement over ‘big-leaf’ models, models that separate the canopy into sunlit and shaded portions (sun/shade models) may not be able to capture important within-canopy variation in terms of leaf dynamics (e.g. seasonal shifts in vertical leaf area distributions, Smith et al. 2019) and functions (e.g. thermal responses, as we present in this paper). Hence, multi-layered ecosystem models may be necessary for accurately projecting future forest function.

(Nakamura *et al.*, 2017)–> modelling ideas?

*(do we need a section on ecosystem function– e.g., transpiration, gpp?)*

### Implications for climate change responses

* CO2 may lead to denser understory (Martijn)
* Influence of increasing temperatures on species compositions and feedbacks to future forest microclimates and function?

–Variation across horizontal biophysical gradients (climate, soils, etc.)(E.O)

## Conclusions

## SI files

Appendix S1. Methods for NEON vertical profiles

Appendix S2. Methods for literature review

Appendix S3. Methods for SCBI tree-ring analysis

## References

Allen CD**,** Breshears DD**,** McDowell NG. **2015**. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere* **6**: art129.

Bennett AC**,** McDowell NG**,** Allen CD**,** Anderson-Teixeira KJ. **2015**. Larger trees suffer most during drought in forests worldwide. *Nature Plants* **1**: 15139.

Bolstad PV**,** Mitchell K**,** Vose JM. **1999**. Foliar temperature–respiration response functions for broad-leaved tree species in the southern Appalachians. *Tree Physiology* **19**: 871–878.

Bonan GB. **2016**. *Ecological climatology: Concepts and applications*. New York, NY, USA: Cambridge University Press.

Campbell G**,** Norman J. **1998**. *An Introduction to Environmental Biophysics*. New York: Springer.

Chazdon RL**,** Fetcher N. **1984**. Photosynthetic Light Environments in a Lowland Tropical Rain Forest in Costa Rica. *Journal of Ecology* **72**: 553–564.

Chen X**,** Sun J**,** Wang M**,** Lyu M**,** Niklas KJ**,** Michaletz ST**,** Zhong Q**,** Cheng D. **2020**. The Leaf Economics Spectrum Constrains Phenotypic Plasticity Across a Light Gradient. *Front. Plant Sci.* **11**.

Curtis EM**,** Knight CA**,** Leigh A. **2019**. Intracanopy adjustment of leaf-level thermal tolerance is associated with microclimatic variation across the canopy of a desert tree (Acacia papyrocarpa). *Oecologia* **189**: 37–46.

Davis KT**,** Dobrowski SZ**,** Holden ZA**,** Higuera PE**,** Abatzoglou JT. **2019**. Microclimatic buffering in forests of the future: The role of local water balance. *Ecography* **42**: 1–11.

De Frenne P**,** Rodríguez-Sánchez F**,** Coomes DA**,** Baeten L**,** Verstraeten G**,** Vellend M**,** Bernhardt-Römermann M**,** Brown CD**,** Brunet J**,** Cornelis J ***et al.*** **2013**. Microclimate moderates plant responses to macroclimate warming. *Proc Natl Acad Sci U S A* **110**: 18561–18565.

Doughty CE**,** Goulden ML. **2008**. Are tropical forests near a high temperature threshold? *Journal of Geophysical Research: Biogeosciences* **113**.

Fauset S**,** Freitas HC**,** Galbraith DR**,** Sullivan MJP**,** Aidar MPM**,** Joly CA**,** Phillips OL**,** Vieira SA**,** Gloor MU. **2018**. Differences in leaf thermoregulation and water use strategies between three co-occurring Atlantic forest tree species. *Plant, Cell & Environment* **41**: 1618–1631.

Feeley K**,** Martinez-Villa J**,** Perez T**,** Silva Duque A**,** Triviño Gonzalez D**,** Duque A. **2020**. The Thermal Tolerances, Distributions, and Performances of Tropical Montane Tree Species. *Frontiers in Forests and Global Change* **3**.

Harley P**,** Guenther A**,** Zimmerman P. **1996**. Effects of light, temperature and canopy position on net photosynthesis and isoprene emission from sweetgum (Liquidambar styraciflua) leaves. *Tree Physiol* **16**: 25–32.

Huang M**,** Piao S**,** Ciais P**,** Peñuelas J**,** Wang X**,** Keenan TF**,** Peng S**,** Berry JA**,** Wang K**,** Mao J ***et al.*** **2019**. Air temperature optima of vegetation productivity across global biomes. *Nature Ecology & Evolution* **3**: 772–779.

Kafuti C**,** Bourland N**,** De Mil T**,** Meeus S**,** Rousseau M**,** Toirambe B**,** Bolaluembe P-C**,** Ndjele L**,** Beeckman H. **2020**. Foliar and Wood Traits Covary along a Vertical Gradient within the Crown of Long-Lived Light-Demanding Species of the Congo Basin Semi-Deciduous Forest. *Forests* **11**: 35.

Martin RE**,** Asner GP**,** Bentley LP**,** Shenkin A**,** Salinas N**,** Huaypar KQ**,** Pillco MM**,** Ccori Álvarez FD**,** Enquist BJ**,** Diaz S ***et al.*** **2020**. Covariance of Sun and Shade Leaf Traits Along a Tropical Forest Elevation Gradient. *Front. Plant Sci.* **10**: 1810.

Martin TA**,** Hinckley TM**,** Meinzer FC**,** Sprugel DG. **1999**. Boundary layer conductance, leaf temperature and transpiration of Abies amabilis branches. *Tree Physiology* **19**: 435–443.

Mau A**,** Reed S**,** Wood T**,** Cavaleri M. **2018**. Temperate and Tropical Forest Canopies are Already Functioning beyond Their Thermal Thresholds for Photosynthesis. *Forests* **9**: 47.

McDowell N**,** Pockman WT**,** Allen CD**,** Breshears DD**,** Cobb N**,** Kolb T**,** Plaut J**,** Sperry J**,** West A**,** Williams DG ***et al.*** **2008**. Mechanisms of plant survival and mortality during drought: Why do some plants survive while others succumb to drought? *New Phytologist* **178**: 719–739.

McGregor I**,** Helcoski R**,** Kunert N**,** Tepley AJ**,** Gonzalez-Akre EB**,** Herrmann V**,** Zailaa J**,** Stovall AEL**,** Bourg NA**,** McShea WJ ***et al.*** Tree height and drought tolerance traits shape growth responses across droughts in a temperate broadleaf forest. *Target journal: New Phytologist*.

Michaletz ST**,** Weiser MD**,** McDowell NG**,** Zhou J**,** Kaspari M**,** Helliker BR**,** Enquist BJ. **2016**. The energetic and carbon economic origins of leaf thermoregulation. *Nature Plants* **2**: 16129.

Muir CD. **2019**. Tealeaves: An R package for modelling leaf temperature using energy budgets. *AoB PLANTS* **11**.

Nakamura A**,** Kitching RL**,** Cao M**,** Creedy TJ**,** Fayle TM**,** Freiberg M**,** Hewitt CN**,** Itioka T**,** Koh LP**,** Ma K ***et al.*** **2017**. Forests and Their Canopies: Achievements and Horizons in Canopy Science. *Trends in Ecology & Evolution* **32**: 438–451.

Niinemets Ü**,** Anten NPR. **2009**. Packing the Photosynthetic Machinery: From Leaf to Canopy. In: Laisk A, Nedbal L, Govindjee, eds. Advances in Photosynthesis and Respiration. Photosynthesis in silico: Understanding Complexity from Molecules to Ecosystems. Dordrecht: Springer Netherlands, 363–399.

Niinemets Ü**,** Keenan TF**,** Hallik L. **2015**. A worldwide analysis of within-canopy variations in leaf structural, chemical and physiological traits across plant functional types. *New Phytologist* **205**: 973–993.

Niinemets Ü**,** Kull O**,** Tenhunen JD. **2004**. Within-canopy variation in the rate of development of photosynthetic capacity is proportional to integrated quantum flux density in temperate deciduous trees. *Plant, Cell & Environment* **27**: 293–313.

Niinemets Ü**,** Sun Z. **2015**. How light, temperature, and measurement and growth [CO2] interactively control isoprene emission in hybrid aspen. *J Exp Bot* **66**: 841–851.

Niinemets Ü**,** Valladares F. **2004**. Photosynthetic Acclimation to Simultaneous and Interacting Environmental Stresses Along Natural Light Gradients: Optimality and Constraints. *Plant Biology* **6**: 254–268.

Ozanne CMP**,** Anhuf D**,** Boulter SL**,** Keller M**,** Kitching RL**,** Körner C**,** Meinzer FC**,** Mitchell AW**,** Nakashizuka T**,** Dias PLS ***et al.*** **2003**. Biodiversity Meets the Atmosphere: A Global View of Forest Canopies. *Science* **301**: 183–186.

Perkins SE**,** Alexander LV**,** Nairn JR. **2012**. Increasing frequency, intensity and duration of observed global heatwaves and warm spells. *Geophysical Research Letters* **39**.

Poorter H**,** Niinemets Ü**,** Ntagkas N**,** Siebenkäs A**,** Mäenpää M**,** Matsubara S**,** Pons T. **2019**. A meta-analysis of plant responses to light intensity for 70 traits ranging from molecules to whole plant performance. *New Phytol.* **223**: 1073–1105.

Rey-Sánchez A**,** Slot M**,** Posada J**,** Kitajima K. **2016**. Spatial and seasonal variation in leaf temperature within the canopy of a tropical forest. *Climate Research* **71**: 75–89.

Roberts J**,** Cabral OMR**,** Aguiar LFD. **1990**. Stomatal and Boundary-Layer Conductances in an Amazonian terra Firme Rain Forest. *The Journal of Applied Ecology* **27**: 336.

Sack L**,** Melcher PJ**,** Liu WH**,** Middleton E**,** Pardee T. **2006**. How strong is intracanopy leaf plasticity in temperate deciduous trees? *American Journal of Botany* **93**: 829–839.

Scheffers B**,** Edwards D**,** Diesmos A**,** Williams S**,** Evans T. **2013**. Microhabitats reduce animal’s exposure to climate extremes. *Global change biology* **20**.

Senf C**,** Pflugmacher D**,** Zhiqiang Y**,** Sebald J**,** Knorn J**,** Neumann M**,** Hostert P**,** Seidl R. **2018**. Canopy mortality has doubled in Europe’s temperate forests over the last three decades. *Nature Communications* **9**: 4978.

Senf C**,** Seidl R. **2020**. Mapping the forest disturbance regimes of Europe. *Nature Sustainability*: 1–8.

Sharkey TD**,** Monson RK. **2014**. The future of isoprene emission from leaves, canopies and landscapes. *Plant, Cell & Environment* **37**: 1727–1740.

Smith MN**,** Stark SC**,** Taylor TC**,** Ferreira ML**,** Oliveira E de**,** Restrepo‐Coupe N**,** Chen S**,** Woodcock T**,** Santos DB dos**,** Alves LF ***et al.*** **2019**. Seasonal and drought-related changes in leaf area profiles depend on height and light environment in an Amazon forest. *New Phytologist* **222**: 1284–1297.

Stark SC**,** Breshears DD**,** Aragón S**,** Villegas JC**,** Law DJ**,** Smith MN**,** Minor DM**,** Assis RL de**,** Almeida DRA de**,** Oliveira G de ***et al.*** **2020**. Reframing tropical savannization: Linking changes in canopy structure to energy balance alterations that impact climate. *Ecosphere* **11**: e03231.

Storck P**,** Lettenmaier DP**,** Bolton SM. **2002**. Measurement of snow interception and canopy effects on snow accumulation and melt in a mountainous maritime climate, Oregon, United States. *Water Resources Research* **38**: 5–1–5–16.

Stovall AEL**,** Shugart H**,** Yang X. **2019**. Tree height explains mortality risk during an intense drought. *Nature Communications* **10**: 4385.

Suggitt A**,** Wilson R**,** Isaac N**,** Beale C**,** Auffret A**,** August T**,** Bennie J**,** Crick H**,** Duffield S**,** Fox R ***et al.*** **2018**. Extinction risk from climate change is reduced by microclimatic buffering. *Nature Climate Change* **8**.

Thom D**,** Sommerfeld A**,** Sebald J**,** Hagge J**,** Müller J**,** Seidl R. **2020**. Effects of disturbance patterns and deadwood on the microclimate in European beech forests. *Agricultural and Forest Meteorology* **291**: 108066.

Tymen B**,** Vincent G**,** Courtois EA**,** Heurtebize J**,** Dauzat J**,** Marechaux I**,** Chave J. **2017**. Quantifying micro-environmental variation in tropical rainforest understory at landscape scale by combining airborne LiDAR scanning and a sensor network. *Annals of Forest Science* **74**: 32.

Yang PC**,** Black TA**,** Neumann HH**,** Novak MD**,** Blanken PD. **1999**. Spatial and temporal variability of CO2 concentration and flux in a boreal aspen forest. *Journal of Geophysical Research: Atmospheres* **104**: 27653–27661.

Zellweger F**,** Coomes D**,** Lenoir J**,** Depauw L**,** Maes SL**,** Wulf M**,** Kirby KJ**,** Brunet J**,** Kopecký M**,** Máliš F ***et al.*** **2019**. Seasonal drivers of understorey temperature buffering in temperate deciduous forests across Europe (A Algar, Ed.). *Global Ecology and Biogeography* **28**: 1774–1786.

Zellweger F**,** De Frenne P**,** Lenoir J**,** Vangansbeke P**,** Verheyen K**,** Bernhardt-Römermann M**,** Baeten L**,** Hédl R**,** Berki I**,** Brunet J ***et al.*** **2020**. Forest microclimate dynamics drive plant responses to warming. *Science* **368**: 772–775.

Zhang J-L**,** Poorter L**,** Hao G-Y**,** Cao K-F. **2012**. Photosynthetic thermotolerance of woody savanna species in China is correlated with leaf life span. *Annals of Botany* **110**: 1027–1033.