**Title:** Thermal sensitivity of canopy versus understory leaves: patterns, mechanisms, and ecological implications

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## Abstract

## Introduction

**As the climate warms, understanding forest responses to temperature is critical.**

**Forest canopy microclimate buffering is emerging as important for forest ecology in an era of climate change.** Forest canopies buffer temperatures and other conditions - Zellweger *et al.* (2020)

We’re seeing increasing evidence that this impacts the ecology, with potential feedbacks to climate change. - Zellweger *et al.* (2020) - (Suggitt et al. 2018, Scheffers et. al 2014) - Larger trees suffer more during drought (Bennett et al. 2015) and may be partially influenced by temperature

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

This review addresses the following questions:

1. How does the biophysical environment vary with height in forests?
2. How do leaf traits vary with height (or between sun and shade leaves) in forests?
3. How do biophysical environment and traits combine to affect leaf temperature?
4. How does leaf metabolism respond to temperature in canopy and understory settings?
5. What are the implications of these patterns for the ecology and climate change responses of canopy versus understory trees?

*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), we also review studies focused on exposure gradients.*



**Figure 1. (schematic of a forest summarizing most important gradients.** Current fig is just a rough illustration of how this might look – a draft figure that KAT had on hand illustrating hypotheses (ignore specific content). 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).

## The biophysical environment

**Forest canopies have a buffering effect on multiple aspects of the understory climate (Fig.** 2**).** Most notably, solar radiation decreases along a vertical profile from the top of the canopy to the forest floor (Fig. **2x**). - *Bonan (2016) reviews this and points to appropriate references* - (Mau et al. 2018?) - Sunflecks: Leaky et al. 2003?

Wind speeds are also higher at the top of the canopy (Fig. **2x**). - *(find some good refs for this/ fill in more specifics)* - McGregor *et al.* This results in higher boundary layer conductance, *DEFINE*, for canopy leaves (Martin *et al.*, 1999).

Air temperature, , is sometimes signficantly 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). 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 (McGregor *et al.*).

Humidity also varies across the forest vertical profile, being generally higher in the understory (Fig. **2x**). - DETAILS - REFS - McGregor *et al.* RH, in combination with temperature, determines vapor pressure deficit, - is lower in understory of Atlantic forest during wet season (Fauset et al. 2018) This means that canopy leaves tend to be exposed to higher *evaporative demand*.

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. 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-review paper, showing NEON data from SCBI. See issue 2: <https://github.com/EcoClimLab/vertical-thermal-review/issues/2>.

**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 (Zellweger *et al.*, 2019) - (Thom *et al.*, 2020) *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). SCA species increase T buffering (Zelllweger et al. 2019) (Zellweger *et al.*, 2019) 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)

## Trait variation

## Leaf temperature

Many of the biophysical and trait variable reviewed above affect leaf temperature, , which 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. 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.

 Aligning with biophysical expectations, field observations have show that leaf temperatures are influenced by the biophysical environment and leaf traits. 1. Air T 2. Solar radiation 3. Leaf traits

When vertical gradients in the biopgysical 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).

## Leaf metabolism and thermal stress

## Ecology



**Figure 4. Temperature sensitivity of tree growth for understory versus canopy trees.** Data from Helcoski et al. 2019.

## Future Questions

## Conclusions

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