**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 demography and ecosystem function. Strong vertical microclimatic gradients imply that canopy leaves are exposed to more solar radiation and higher evaporative demand than understory leaves, particularly in forests with dense canopies. However, foliar traits relevant to shaping leaf temperature () and metabolism also vary strongly across height or light gradients. Resulting ’s exceed air temperature () under conditions of high solar radiation, low wind, and low stomatal conductance. Differences are most pronounced when hydraulic limitations impede evaporative cooling such that ’s of sun-exposed canopy leaves become dramatically elevated above both and understory . 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

**Forest responses and feedbacks to climate change will have a critical influence on the future of Earth’s climate.** Globally, temperatures have risen # C since YEAR and are expected to rise an additional #-#C by YEAR (IPCC 2021), accompanied by increasing severity and frequency of heat waves (Perkins *et al.*, 2012) and hotter droughts [*Trenberth et al. 2014*]. These changes are expected to have profound effects on tree metabolism and forest ecosystem function (Breshears *et al.*; IPBES report), including altered rates of photosynthesis and respiration (Breshears *et al.*, p. 2021), foliar damage during heat waves (O’sullivan *et al.*, 2017), and reduced growth and elevated mortality during drought (Teskey *et al.*, 2015; Breshears *et al.*). Individually or in combination, these changes have the potential to reduce forest C sequestration, as may already be occurring in some forests (REFS; Sullivan *et al.*, 2020). The resulting feedbacks to the climate system (e.g., decreased C storage, altered albedo and hydrology) will in turn have a critical influence on the future trajectory of climate change (Bonan, 2016, Bonan 2008), yet this influence remains extremely uncertain [REFS].

**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).** Forests are vertically and horizontally stratified, with trees of different sizes through various successional stages. Overstory trees form canopies that play a crucial role in moderating macro-microclimate (Nakamura *et al.*, 2017; Ozanne *et al.*, 2003) by buffering extreme temperatures along with other macroclimatic conditions in the understory. This creates a vertical stratification of biophysical environmental conditions such as temperature, light, wind, humidity and CO2 that influences leaf traits, thermoregulation and metabolism along the gradient, with implications for whole plant performance (Fauset *et al.*, 2018; Michaletz *et al.*, 2016). Despite the fact that this vertical gradient inevitably shapes nearly every aspect of plant metabolism, demography, and ecology, we lack comprehensive understanding of these gradients. *(Niinemets et al. (2004) highlights how biophysical and photosynthetic gradients vary along the vertical canopy profile, however our current knowledge of this topic is lacking.)* Importantly, this limits our ability to understand how warming temperatures will affect leaf-level metabolism, whole-plant performance, and, in turn, forest ecology and biodiversity, energy balance, ecosystem function, and biosphere-atmosphere interactions.

**Here, we review how the biophysical environment and biological form and function vary across the vertical canopy gradient in forests.** We focus on five key themes (Fig. 1): (1) the biophysical environment; (3) leaf temperature (); (2) the leaf traits most strongly influence leaf temperature and metabolism; (4) foliar metabolism, including stomatal conductance, photosynthesis, respiration, and volatile organic compound (VOC) production; and (5) size-structuring of whole-tree and ecosystem function. *We then consider the implications for understanding forest responses to global change, including scaling across space and time.*



**Figure 1. DRAFT schematic of a forest summarizing most important gradients–sort of a “graphical abstract”.** [Issue #27](https://github.com/EcoClimLab/vertical-thermal-review/issues/27).

# Review of vertical gradients

## The biophysical environment

**The biophysical environment across the vertical gradient from the forest floor to the the top of the canopy is in large part determined by the structure of the forest itself.** Here, we define the biophysical environment to include the physical structure of the vegetation and associated physical conditions. In this section, we supplement a review of the existing literature with a new analysis of data on vegetation structure and vertical microclimate profiles from the U.S. National Ecological Observatory Network [NEON; Appendix S1, Schimel et al. 2007].

### Foliage density

**Canopy foliage, which is vertically structured in correspondence with the size, structure of trees in the forest, acts as the primary physical barrier between the atmosphere and the forest floor, producing a buffering effect on multiple aspects of the understory conditions (Fig. 2).** Leaf area density…. *description of most common vertical pattern (Bonan (2016) reviews this and points to appropriate references)* Vertical profiles in leaf area density vary across forests, being… *summarize some key differences across forest types* (REFS), and are altered (*HOW?*) following disturbance (e.g., Parker *et al.*, 2002 ; Stark *et al.*, 2020; Almeida *et al.*, 2016 ). They also vary seasonally, … (Parker & Tibbs 2004; Smith *et al.* (2019) ; Parker *et al.* (2019)). In mixed deciduous- evergreen broadleaf forests, the fraction of deciduous trees tends to increase across tree size classes (Condit, Meakem, ?any work on this in temperate forests??). In this review, we focus primarily on growing season conditions, including leaf phenology at the edges of the growing season, but excluding periods when no leaves are present in deciduous forests.



**Figure 2. Vertical gradients in the biophysical environment for six sites in the National Ecological Observatory Network (NEON)**. Shown are height profiles in growing season (a) leaf area density, (b) proportion light incidence, (c) proportion sun leaves, and July mean ± 1 standard deviation for (d) maximum photosyntehtically active ratiation (PAR), (e) maximum wind speed, (f) minimum humidity, (g) maximum , and (h) maximum biological temperature, . Sites include a tropical broadleaf evergreen forest (Pu‘u Maka‘ala Natural Area Reserve, Hawaii; PUUM), a subtropical longleaf pine savanna (Ordway-Swisher Biological Station, FL; OSBS), two temperate broadleaf forests (Smithsonian Conservation Biology Institute, VA, SCBI; Smithsonian Environmental Research Center, MD, SERC), and a mixed northern hardwood and coniferous forest (Harvard Forest, MA; HARV). ([issue 20](https://github.com/EcoClimLab/vertical-thermal-review/issues/20))

### Light environments

**Light conditions, specifically changes in the proportion of incident light and photosynthetically active radiation (PAR), vary along the vertical gradient with leaf area index (LAI), canopy height, canopy structure, and across species and forest types (Fig. 2; Koike *et al.*, 2001).** Generally, along a vertical gradient in forests globally, amount of light decreases from canopy tops to the forest floor. This trend is mediated by foliage LAI and density, where the gradient is more prounced in broad-leaf forests than needle-leaf forests [Fig. 2; Aussenac (2000); von Arx *et al.* (2012); Chazdon & Fetcher, 1984; Smith et al., 2019; Tymen et al., 2017]. Light reaching forest floors that is incident to canopy tops ranges from ~1-2% in tropical forests (Chazdon & Fetcher, 1984; Roberts *et al.*, 1990; Parker *et al.*, 2019), 4-5% in mixed-wood boreal and northern temperate forests(Bartemucci *et al.*, 2006) to 17-34% in needle-leaf forests (Baldocchi *et al.*, 1997). Sunflecks, caused by small canopy gaps and wind-induced canopy movements also contribute to the shaded forest regions that receive 50-80% of their light for photosynthesis during these short exposures (Way & Pearcy, 2012). Additionally, in heterogeneous canopies [with high gap fractions and large variation in tree height], the distance from the outer canopy to the inner canopy is a better proxy for light environment than height (Parker 1995).

### Wind speeds

**Wind speeds are also higher at the top of the canopy (Figs. 2, S1-S#), owing to… (Jucker *et al.*, 2018).** Across all **#** forested NEON sites, wind speeds increased with height, with daily maximum wind speeds at the top of the averaging up to **#** m s-1 higher at the top of the vertical profile than at the bottom. Consistent with these results, higher wind speeds at greater heights have been observed in both closed-canopy forests (**???**; McGregor *et al.*) and open savannas (Curtis *et al.*, 2019).

### Air temperature

**Air temperature, , is sometimes significantly buffered by forest canopies (Fig. 2).** Studies comparing under forest canopies with nearby clearings have found lower maximum temperatures under forest canopies globally (De Frenne *et al.*, 2019).

The strength of this buffering is greater under dense-canopy than open-canopy forests; with daytime cooler lower maximum temperature, and nighttime warmer higher minimum in the understory, relatively more than open-forests, nearby clearings (*Defrenne et al. 2021*; von Arx *et al.*, 2012, p. Defrenne et al. 2021; **???**; Rambo & North, 2009; Zellweger *et al.*, 2019) and neighboring tree crop agricultural plantations (Jucker *et al.*, 2018; Hardwick *et al.*, 2015). On the other hand, open-forests maintain higher daytime maximum temperature in the understory closer to nearby clearings (Martin *et al.*, 1999; Rambo & North, 2009; von Arx *et al.*, 2012; De Frenne *et al.*, 2019) and sometimes warmer nighttime understory temperatures than above canopy, due to long wave infrared radiation from the soil (von Arx *et al.*, 2012).

Seasonally, buffering capacity increases with water availablity (Davis *et al.*, 2019) and is greater in wet than dry season (Fauset *et al.*, 2018, Tymen et al. 2017; von Arx *et al.*, 2012; Rey-Sánchez *et al.*, 2016; McGregor *et al.*). However, under colder conditions, dense-canopies maintain warmer higher minimum temperatures [] in the understory relative to open-canopy forests and nearby clearings (Zellweger *et al.*, 2019; *Defrenne et al. 2021*; Nakamura *et al.*, 2017; McGregor *et al.*) where greater radiative heat loss in exposed areas results in lower .

Tree height also plays a role in buffering where trees upto 20m with higher LAI can maintain lower mean and max temperature and vapor pressure deficit () in the understory. However, beyond a certain tree height, temperature and offset can plateau (Jucker *et al.*, 2018; Hardwick *et al.*, 2015).

### Humidity and evaporative demand

**Humidity also varies across the forest vertical profile, and is generally higher in the understory (Fig. 2).**(McGregor *et al.*) Along with temperature, dense-canopy forests maintain higher daily maximum relative humidity () below-canopy than open-forests and nearby open areas, which is greater in wetter conditions, in warmer than colder months (von Arx *et al.*, 2012). RH, in combination with temperature, determines , an important metric expressing the driving force of water loss from a leaf; tends to be greater in upper-canopy and canopy gaps than in the understory (Niinemets & Valladares, 2004; Fauset *et al.*, 2018; Tymen *et al.*, 2017).

### Carbon dioxide

**Atmopsheric carbon dioxide (CO2) concentrations tend to be higher near ground level at night, but largely dissipate during the day (Yang *et al.*, 1999; Koike *et al.*, 2001).** Given that differences are small during the day when photosynthesis is occurring, and that even nighttime differences are modest at the height of understory tree crowns, CO2 concentrations are unlikely to have much of an effect on the energy balance and metabolism of leaves across the forest vertical gradient.

### Geographic and climatic factors

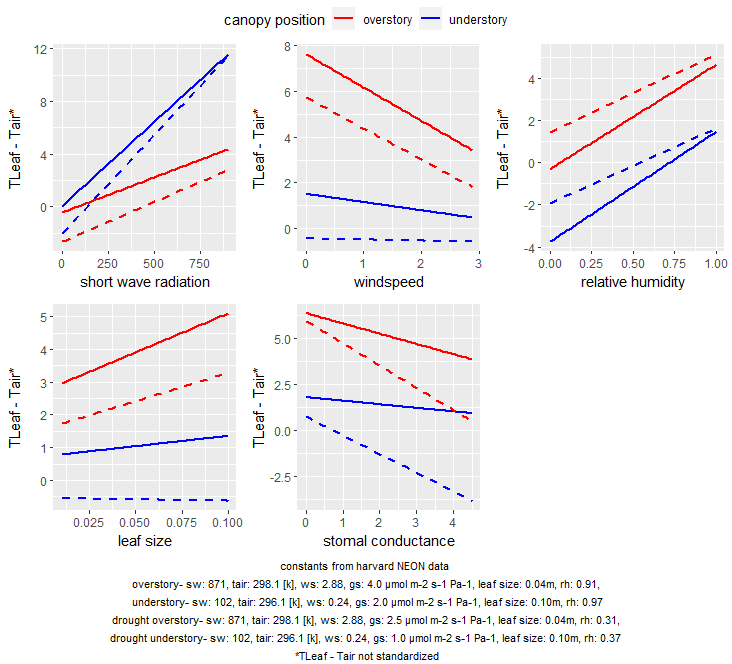
With altitude, the strength of buffering decreases, moving to open-forests (von Arx *et al.*, 2012; Zellweger *et al.*, 2019; Rajsnerová *et al.*, 2015; Liang *et al.*, 2019), greater in wetter than drier regions [**REF**] and increases with proximity to water, for eg. in riparian forests. (Davis *et al.*, 2019; Macek *et al.*, 2019)

## Leaf temperature

### Biophysical drivers

**The combination of biophysical variables reviewed above drive leaf temperature distribution along the vertical gradient, which in turn has a strong influence on leaf metabolism (see following section).** Leaves adapt to their biophysical environment to maximize carbon assimilation, by maintaining optimum in a given circumstance (Perez & Feeley, 2020; Michaletz *et al.*, 2015). As a result, leaves can be cooler than air at high temperature and warmer than air at low temperature (‘limited homeothermy’) or can be drastically warmer than (‘megathermy’). In some cases, can be equalled to (‘poikilothermy’) (Cavaleri, 2020; Drake *et al.*, 2020).

itself is determined by the energy balance of a leaf, influenced by leaf traits, and can be estimated based on basic biophysical principles (Campbell & Norman, 1998; Michaletz *et al.*, 2016; Muir, 2019) (Fig. 3). The difference between and is determined as a function of energy input (through radiation or heat) versus heat lost (such as transpiration) to the environment (Fig. 2; Michaletz *et al.*, 2015).



**Figure 3. Theoretical expectations for variation in the elevation of above in response to (a) shortwave radiation, (b) wind speed, (c) relative humidity, (d) leaf width, and (e) stomatal conductance.** Leaf temperatures were modeled using the tealeaves R package of Muir (2019) parameterized to represent typical conditions for a broadleaf species (*Quercus rubra*) in a mesic temperate forest (Harvard Forest, Massachusetts, USA), as detailed in Appendix S2. [ISSUE #6](https://github.com/EcoClimLab/vertical-thermal-review/issues/6).

Leaf thermoregulation is a tradeoff between water use strategy and optimum (Fauset *et al.*, 2018; Koch *et al.*, 1994). Leaves can regulate their temperature by dissapating heat through stomatal conductance (), even in drastic biophysical conditions [**REF**] but when leaf water demand exceeds water transport, driven by irradiance, , VPD or drought, conservation of water ( limitation) occurs at the cost of increasing .

Incoming solar radiation is a strong driver of , relative to . With maximum , leaves can maintain similar to at high radiation loads, but limitation can cause solar radiation to substantially elevate greater than (Cavaleri, 2020).

Greater wind speed (Fig. 2) decreases - by increasing boundary layer conductance () (Daudet *et al.*, 1999). Therefore, under hot conditions, canopy-leaves exposed to higher wind speeds would be most effective at cooling with high [Drake et al. 2018]. At low wind conditions, small to heat transfer can increase - (Leigh *et al.*, 2017; Martin *et al.*, 1999) where boundary layer resistance increases with thickness of air layer at the leaf surface. This tends to be greater in buffered leaves (Roberts *et al.*, 1990; Martin *et al.*, 1999; Stokes *et al.*, 2006)

**(paragraph on hydraulics as a driver of leaf T:e.g., water on leaves - evaporative cooling - and leaf water content)** While stomatal conductance is inherently greater in exposed leaves than buffered shaded leaves, factors driving limitation–irradiance, VPD and –are also greater with exposure. As a result, exposed leaves can experience steeper limitation than buffered leaves, driving an increase in , further influenced by irradiance and (Leigh *et al.* (2017); Fauset *et al.* (2018)). On the other hand, due to inherently lower in shade leaves, they can remain cooler under buffered conditions and substantially warmer under increased or irradiance.

**In addition, leaf size and morphology, which vary dramatically across the vertical gradient (reviewed in following section), impact and therefore leaf temperature.** Smaller leaves remain within a few degrees of , *with coolest leaves at intermediate sizes (~10mm)* due to higher to heat transfer (Leigh *et al.*, 2017; Bauerle & Bowden, 2011). Whereas, large leaves (with greater leaf width) can be significantly cooler than under low radiation with stomata open, and significantly hotter under high radiation or with stomata closed (Leigh *et al.*, 2017; Fauset *et al.*, 2018).

### In-situ observations

**Vertical profiles in microclimate (Fig. 2), leaf traits (see following section), and *evapotranspiration* (*where is this discussed? and do we say anything about evaporation?*) together shape in-situ leaf temperatures according to the principles outlined above (Fig. 3).** Canopy buffering capacity largely influences vertical dynamics. Particularly, in open-forests with lower buffering capacity, is greater in lower-canopy than upper canopy, reflecting microclimate conditions of vertical air mixing, light permeating through canopy layers, still air in the lower canopy and heating from the ground, (Hadley & Smith, 1987; Martin *et al.*, 1999; Rey-Sánchez *et al.*, 2016; Zweifel *et al.*, 2002; Muller *et al.*, 2021). Similarly, trees growing close to the ground can experience greater heat stress in their lower than upper canopies (Hadley & Smith, 1987; Curtis *et al.*, 2019). Greater in inner canopy can also increase relatively more than upper-canopy (Dietz *et al.*, 2007). Under other conditions tracks and therefore differs little between understory and canopy (Fig. 2).

**However, canopy leaves can reach much higher maximum , and higher , than understory leaves.** Closed-canopy forests, such as tropical and semi-deciduous tropical, and temperate forests, experience greater and higher maximum in the upper canopies due to greater heat and water stress from limitation, than buffered lower-canopies (Doughty & Goulden, 2008; Fauset *et al.*, 2018; Rey-Sánchez *et al.*, 2016; Mau *et al.*, 2018b,b; Miller *et al.*, 2021). Greater light input in exposed upper-canopy leaves can sometimes increase beyond temperature optimum for photosynthesis () and making upper-canopies susceptible to heat stress (Doughty & Goulden, 2008; Mau *et al.*, 2018b). Comparing forests, upper-canopies of temperate-deciduous species can have greater - than the upper-canopies of tropical moist and wet forest species (Mau *et al.*, 2018b).

### Leaf traits

**Leaf thermoregulation largely depends leaf traits, that are in-turn adapted to their environment (Michaletz *et al.*, 2016). Therefore, are critical in maintaining desirable and in shaping leaf metabolism (following section) across forest vertical strata (Figs. 2, S1-S#)(Zwieniecki *et al.*, 2004; Michaletz *et al.*, 2015)**

Leaf morphological adaptation to the local microenvironement takes place during leaf expansion (Zwieniecki *et al.*, 2004). Degrees of direct to diffused light and resultant water demands shape sun vs. shade leaves and their necessary vascular architecture (Zwieniecki *et al.*, 2004; Casas *et al.*, 2011; Niinemets, 2016; Keenan & Niinemets, 2016). Therefore, taller tree canopy-leaves dramatically vary from canopy-interior and understory due to the differences in biophysical conditions (Figs. 2, S1-S#). While leaf traits vary primarily on the axis of light, at greater tree-heights, both theory and empirical evidence indicate that other factors-for example, tree-height or exposure to evaporative demand (Fig. 2)- are also important in shaping at least a subset of traits.

In particular, hydraulic constraints increase with height on a tree [REFS; *McDowell-isotopes book chapter*; Coble & Cavaleri (2015); *Couvreur et al., 2018*] such that gas exchange is strongly constrained by at the tops of(~100 m. tall *Sequoia sempervirens*; *Ambrose et al. 2009, 2010*). Isolating height (>35m) under constant light conditions show that, canopy decreases along with increasing (Schäfer *et al.*, 2000; Ambrose *et al.*, 2010). Morphologically, leaf size [Kaare H. Jensen and Maciej A. Zwieniecki, 2013] and lobation (Kusi & Karsai, 2020) have shown to decrease, while leaf mass per area (at greater than 20m) to increase (Rijkers *et al.*, 2000; Coble & Cavaleri, 2015; Kenzo *et al.*, 2015; Chin & Sillett, 2017).

Disentangling the influences of hydraulic constraints, light and other biophysical drivers that vary with height (Fig. 2) on leaf traits remains an important area for research, but is beyond the scope of the current review. Our primary interest is in how leaf traits and function vary across the vertical gradient from the top of the canopy to the understory in forests. For the purposes of interpreting the results presented here, we note that patterns across light and height gradients are generally similar, at least in direction (Table 1), but likely to be modified by covarying biophysical constraints.

#### *(clarify intra- vs inter-specific variation - 1 short paragraph)*

Across the vertical gradient, traits vary (1) across sun and shade leaves within individuals, (2) across canopy and understory individuals of the same species, and (3) across canopy and understory species. The majority of studies characterizing variation in leaf traits or metabolism examine intraspecific patterns (categories 1 and 2), which are therefore the main focus of this review (Table 1). However, when it comes to understanding and modeling forest ecosystem function, the relevant scale of variation is interspecific (e.g., *Lamour, Serbin in prep*).

### Intraspecific variation

Within-canopy gradient of individuals, leaf traits vary–going from buffered [shaded] to exposed canopy positions (Casas *et al.*, 2011)– and therefore exhibit patterns in leaf anatomical, structural and biochemical traits (Sack *et al.*, 2006; Niinemets *et al.*, 2015a; Chen *et al.*, 2020). These trait-patterns contribute to [understanding] dynamics across the gradient (Fauset *et al.*, 2018; Michaletz *et al.*, 2016) where Table 1 summarizes relevant traits for thermal sensitivity. The characterization of trait relationships and leaf responses through the whole vertical canopy is becoming a strong research need because LES theory was developed using mainly sun exposed (upper canopy) leaves (Chen *et al.*, 2020; Keenan & Niinemets, 2016).



Table 1. (*For latest version of table, see tables.pdf.*)

#### Morphological traits

Going from shaded to exposed canopy position, morphological adaptation to dissapate heat increases. Sun leaves are often thicker, smaller, hairier, with greater dissection–lobes and serration–(Sack *et al.*, 2006; Leigh *et al.*, 2017; VOGEL, 1970), hydraulically efficient [Brodribb et al. 2010], with more vertical leaf angles than shade leaves (Niinemets, 1998). All, collectively regulate -photosynthetic balance. On the other hand, shaded leaves invest more in for light capture than in heat dissapation, therefore have lower convective cooling [(**???**); Leigh *et al.* (2017); Wright et al. 2019]. Additionally, under homogeneous light conditions, sun-leaves in different canopy orientations are shaped on the basis of and stress (Mediavilla *et al.*, 2019).

#### Biochemical and physiological traits

Nitrogen along the vertical gradient, is constantly re-mobilized from senescensed to growing leaves (Niinemets, 2007) where , with LMA, leaf soluble sugars, starch and non-structural carbons are greater [Coble & Cavaleri (2014); Coble *et al.* (2016); Weerasinghe et al. 2014]. Additionally, optimizes to prevent photoinhition in sun leaves during direct light and shade leaves during sunflecks, under available soil nitrogen (Kitao *et al.*, 2018).

##### *(Carotenoids/Xanthophyll cycle pigments)*

Pools of xanthophyll pigments–violaxanthin, antheraxanthin and zeaxanthin [], an antioxidant scavenging function–plays a role in converting excess light into heat energy dissipation, enabling short-term acclimation to high temperature and light (Niinemets *et al.*, 1998; Mathur *et al.*, 2018), increases proportional light gradients.

##### Isoprene production

Isoprene production *capability* increases vertically with light and therefore facilitates high heat tolerance in emitting species’ canopy positons [Sharky]

### Interspecific variation

Across tree-size ontogeny of the same species, while fundamental adaptations to light and water are observed in canopy and understory trees similar to within-species gradient (Thomas & Winner, 2002; Rozendaal *et al.*, 2006; Houter & Pons, 2012), increase in LMA, photosynthetic capcity per area, and stomatal conductance with height are attributed to ontogenetical differences, under constant light conditions (Thomas & Winner, 2002; Houter & Pons, 2012). Across multi-species canopy and understory, trait adaptation to spatio-temporal light and biophysical gradient varies largely with inherent specie-specific trait differences such as leaf shape, size, levels and therefore influences individual . As a result, some species might be more susceptible to heat stress at a vertical gradient than others (Fauset *et al.*, 2018).

#### Leaf lifespan and Deciduousness (“Lifecycle / ecological traits?”)

##### *Leaf lifespan*

*Leaf turnover tends to be greater in the sun (in the tropics), so of your standing stock of leaves (at least in evergreen species) sun leaves should be younger than shade leaves. This is bound to affect metabolism, and may affect other aspects of their performance.*

##### *Deciduousness*

Deciduousness as a leaf trait is an adaptation to water and heat stress. Therefore, can influence biophysical gradient and distribution during leaf-loss (Rey-Sánchez *et al.*, 2016). *In the tropics, among species that can be deciduous, greater proportion of deciduous individuals are in larger size classes that tend to lose their leaves more than understory species that are seldom deciduous. Deciduous species are also more prominent in drier sites compared to wet sites (****???****)*

*Spring and fall leaf phenology in temperate deciduous forests (Augsburger).* Leaf emergence in deciduous forests is delayed with height-ontogeny where understory species leaf-out earlier than canopy trees (Vitasse et al. 2013; Seiwa, 1999).

## 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 and vertical gradient (Table 2).



Table 2. (*For latest version of table, see tables.pdf.*)

### Stomatal conductance

While exposed canopy sun-leaves are equipped to thermoregulate more efficiently than shaded-leaves, they are largely constrained by (Sanches *et al.*, 2010; Hernández *et al.*, 2020); and therefore their ability to photosynthesize as well. During the day, max transpiration rate and increases with height and is greater in the upper canopy compared to shaded canopies (Kosugi & Matsuo, 2006; Sanches *et al.*, 2010). During midday, stomtal closure in exposed leaves increases , and decreases photosynthesis (**???**; Zwieniecki *et al.*, 2004; Sanches *et al.*, 2010).

### Photosynthesis

**Photosynthesis is generally higher in exposed canopy positions– a fact that is both theoretically expected and observed in numerous field studies (Table 2; Niinemets 2007 ; Kenzo et al. 2015 ; Slot et al. 2019; Chen et al. 2020).** This is primarily driven by the greater light available to sun leaves. Photosynthesis increases with increasing irradiance, and saturates at quantum flux density of 400 to 700nm .

In response to the greater light availability, sun leaves have traits allowing greater photosynthetic rates at high light under sufficient nutrient and water conditions, including higher concentration of Rubsico, and multiple layers of palisade parenchyma. Light saturation levels differ between leaves and canopies, with leaves saturating at lower light level than canopies (while a certain amount of light saturates the photosynthetic capacity of the leaf, increasing the amount of light in the canopy may increase photosynthesis in the shaded part of the canopy).The vertical gradient in photosynthetic rates is also influenced by available concentration of N and P (and water availability).

beyond photosynthetic declines photosynthesis due it’s peaked response to temperature. Photosynthesis is commonly found to be maximized at the prevalent ambient growing season conditions (Tan et al. 2017; Slot & Winter (2017)). Beyond the optimum, photosynthesis decreases as a result of stomatal closure and increasing (e.g. Slot & Winter (2017); Smith et al. 2020 [temperate/boreal refs needed) and eventually due to biochemical constraints (Kumarathunge *et al.* (2019); e.g. Sage & Kubien 2007; Varhammer et al. 2015 ). Heat stress at can cause irreversible damage to photosystem [II] leading to leaf necrosis and eventually leaf death (Baker 2008; Feeley *et al.*, 2020). Leaves in tropical upper canopies have shown to experience in-situ well above on a regular basis. If is not regulated or adapated, heat stress can loss of canopy leaves [**REF**]

**We have very little evidence as to how the temperature sensitivity of photosynthesis compares 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 in Campbell and Norman 1998; *revisit this!*), based on evidence that of increased with irradiance of an upper canopy leaf compared to shaded lower canopy leaf (Niinemets & Valladares, 2004). However, such a trend is not apparent based on the limited number of field studies that have compared temperature sensitivity of photosynthesis in sun and shade leaves. For 3 species in Panama, the optimum temperature for sun leaves tended to be slightly higher than that of shade leaves, but differences were not significant (Slot et al. 2019 ; Hernández *et al.*, 2020).Similar results were shown for of and of tropical sun and shade leaves (Slot *et al.*, 2019; Hernández *et al.*, 2020), and across a vertical gradient of tropical trees (Mau *et al.*, 2018a; Miller *et al.*, 2021), and temperate trees (Mau *et al.*, 2018a).

*If we take geographic gradients as a reliable proxy, we’d expect temperature sensitivities to reflect the environment to which the trees are adapted/ acclimatized.*

**Leaf thermal tolerance (Tcrit/ T50)** is the temperature at which efficiency of photosystem II starts to decrease, based on chlorphyll a flourescence; and represents temperature at which the efficiency of photosystem II had decreased by 50% [Slot et al. 2020]. Leaf thermal tolerances strongly reflect species adaptation to their microenvironment rather than macroclimate conditions [Feeley *et al.* (2020); Slot et al. 2020; Perez and Feely 2020a] and phylogeny [Slot et al. 2020; Perez and Feeley 2020a].

Typical values across latitude and climate are ~45-50C (O’ sullivan et al. 2017). With elevation, and decrease, as seen in tropical forests and across latitudes (O’sullivan *et al.*, 2017; Feeley *et al.*, 2020; Slot *et al.*, 2020), and vary with species (Krause *et al.*, 2010) and leaf traits (Sastry et al. 2018, Zhang *et al.*, 2012; Slot *et al.*, 2020). Species with large leaves, and slow heating and cooling time [higher thermal time constant] showed greater . On the other hand, leaves of species with greater construction costs–greater LMA– had greater compared to species with low LMA (Slot *et al.*, 2020). However, higher photosynthetic heat tolerance does not necessary increase the breadth of leaf thermal safety margin. Rather, Perez & Feeley (2020) found that, across species sun leaves, higher photosynthetic heat tolerance experienced higher maximum leaf temperatures, and showed low optimum temperature for C assimilation [] and therefore had a narrower breadth of thermal safety margins (difference between maximum leaf temperature and )

**Thermal tolerance (e.g., ) varies with exposure, but there are no studies isolating effect of height.** Because and over the years have been predominantly measured on sun leaves; there remains limited information on sun- and shade-leaves and at vertical height gradient.

Knapp et al. 1994 showed that in tall grass prarie gallery forest in Kansas, photosynthetic heat tolerance measured on chinquapin oak (*Quercus muehlenbergii*) that grew in xeric, sunnier conditions was higher by than bur oak (*Quercus macrocarpa*) that grew in shaded mesic conditions. In both species photosynthetic heat tolerance increased seasonally from June to August. However, more recetly Slot *et al.* (2019) found that though was slightly lower for shade than sun-exposed leaves for two of three species in moist tropical forest in Panama, the results weren’t significant, with both measured near ground level.

In other cases, leaf thermal tolerance reflects microclimatic stress along a vertical gradient. For *Acacia Papyrocarpa* (Benth.) trees in an arid region in Australia, higher composite climate stress and indeed, was greater in the lower north-facing canopy than other canopy positions. Greater in lower north-position also correlated with longer leaf thermal time constants, low-wind speed and greater $T\_{air} (Curtis *et al.*, 2019).

We’re not aware of any other studies on this.“we may want to argue that we have no *a priori* reasons to expect thermal tolerance to scale with height per se (or do we?). I think it makes sense to expect variation with light exposure because of the associated differences in temperature you can expect the leaves to be exposed to, but height itself should not affect heat tolerance other than through associated traits perhaps”–Martijn Slot\*

### Respiration

**Similar to photosynthesis, respiration tends to be higher in canopy sun-leaves (Chen et al. 2020), but temperature sensitivity of respiration––shows no definite trend along the gradient [Bolstad *et al.* (1999); Weerasinghe et al.2014].**

Across species in north-eastern oak deciduous forest, conifer temperate rainforest and in *Liquidambara styraciflua* tree, is observed to be greater in upper-canopy leaves than in shaded lower-canopy leaves, with differing values between species (Turnbull *et al.*, 2003; Harley *et al.*, 1996). However, in a lowland tropical Australian forest study, doesnot vary across species vertical profiles (Weerasinghe *et al.*, 2014), and across temperate trees at Coweeta, though with a slight tendency to increase down the canopy relative to upper-canopy leaves as increases (*see their Fig. 1*)(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)*.*). Bolstad *et al.* (1999) also found evidence of acclimation, but there remained a declining trend of respiration with elevation.

Further information from fluxnet global data analysis shows that with temperature increase, foliage photosynthesis and respiration are coupled at different rates upto photosynthetic thermal optimum, beyond this inflection point, photosynthesis declines whereas respiration increases exponentially, therfore, moving from carbon sink to carbon source, independent of water and irradiance (Duffy *et al.*, 2021)

### VOC production

**Isoprene production** High emission rates occur in the mid-canopy, and even from very small statured trees, 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 and temperature; together and independtly?

## Size-structuring within the ecosystem

**Differences across forest vertical gradients in biophysical conditions, plant traits, and metabolism and its thermal responses scale up to affect whole-tree ecology and ecosystem ecology in several ways.** Vertical gradients in the biophysical environment shape which plant strategies, or sets of traits, are competitive in understory versus canopy conditions.

### Demography

**Vertical gradients affect tree recruitment, growth and survival, and how these respond to climatic variation.** More interesting in this context is how these shape differences in the climatic sensitivity of growth and mortality. 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 review those here.* *(although maybe we should put one paragraph?)*

Biophysically, greater , atmospheric demand and low RH can be more stressful for trees, than soil moisture across biomes-including mesic forests, as the former limits surface conductance and evapotranspiration to a greater extent than soil moisture [Oishi et al. 2016]. On the other hand, greater can do the opposite, where it stifles evapotranspiration thereby increasing , particularly in canopy tops where irradiance can have a greater effect (Fig.3; Perez & Feeley, 2018; Tibbitts, 1979). However, soil water loss in conditions of drought effect larger trees more than small trees. Primarily because, greater biophysical evaporative demand in the canopy cannot meet long-distance water transport from ground-level limited soil moisture (Norway spruce study, bennett; McGregor *et al.*).

On the basis of phenology, because understory trees leaf out earlier than canopy [Vitasse et al. 2013], understory growth is more sensitive to annual warming than canopy, showing earlier spring onset and later autumn senescense, particularly in temperate deciduous forests [Zohnner and Renner, 2019]. However, late spring short-term heat waves negatively impact partially- expanded canopy leaves by inducing leaf shedding and decreasing photosynthesis in reflushed leaves, more than understory saplings that are buffered from such conditions [Filewood and Thomas, 2013].

**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 (Fig 4 **???**; Rollinson *et al.*). 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 higher temperatures reduce understorty tree growth in these forests through an indirect mechanism, such as accelerated competition under warmer temperatures. [Increase in humidity?]

Additionally, interacting biophysical and biological stressors show that stress sensitivity is greater in buffered small trees, and decreases where tolerance increases with height, light with available water. Partly because large NSC reserves in taller trees due to available light allow them to tolerate greater number of stressors than buffered trees that are light and NSC limited (Niinemets, 2010)

*In this section we could perhaps also consider differences in biomass distribution between canopy trees an understory plants, and what that may mean for performance at high temperature. What I’m thinking is the temperature sensitivity of respiration that applies to leaves, stems, and roots, and even though thermal acclimation of leaf respiration is common, much less is known about acclimation of stem and root respiration, and incomplete acclimation still increases the respiration load at higher temperature. It is possible that an increased respiration load is more disadvantageous for understory plants because 1), I suspect that a greater fraction of their total biomass is life biomass that respires (as opposed dead heartwood in the stems of big trees), and 2), because they operate closer to their light compensation point, so if they lose more carbon in respiration, they would need to make up for lost carbon in photosynthesis, but might lack sunlight to do so*



\*\*Figure 4. DRAFT tree-rings figure. Current figure shows (a) drought responses as a function of height in a temperate broadleaf forest (SCBI), from McGregor et al. 2020; (b) responses to growing season temperature in eight New England forests, from Rollinson et al. 2020. I’M NOT SURE THIS IS WHAT WE WANT, BUT I THINK SOME SORT OF TREE-RING FIGURE WOULD BE GOOD. [ISSUE # 29](https://github.com/EcoClimLab/vertical-thermal-review/issues/29).

### C and water flux

*(here, it would be good to add some content on contributions to C cycling across the vertical gradient. If Camille’s paper is published ahead of this, that would be the best source. Meakem et al. 2018, New Phyt has a similar analysis for 3 sites.)*

Leaf-scale properties and processes aggregate non-linearly in vertical and horizontal space, influencing stand-level ecosystem processes, and in turn biosphere-atmosphere exchanges of water, carbon, energy, and trace gases. As described above, variation in temperature across vertical gradients can interact with local light conditions and other vertically varying meteorological conditions to affect species composition (e.g., see Nakamura *et al.* (2017)), leaf traits, and photosynthesis . Linked to this local biophysical variation is the partitioning of evapotranspiration () into soil evaporation, canopy evaporation, and transpiration, which occur across varying spatiotemporal scales depending on light availability, water stress, stomatal physiology, and turbulent transfer (Lawrence et al. 2007, Staudt et al. 2011). Vertical microclimate gradients interact with vertical variation in foliage density, influencing not only the location of evapotranspiration in the canopy, but also differences in rates and net gross primary productivity (, Banerjee & Linn 2018). It has been demonstrated that net carbon assimilation and transpiration can vary substantially for forest canopies with the same LAI but different leaf area density distributions (e.g., Katul et al 2004 , Banerjee & Linn 2018). Further, although transpiration tends to be the dominant component of ET, partitioning is more complex in open canopies where soil evaporation can become more dominant (Baldocchi et al. 2004, Ma et al. 2020), likely affecting vertical thermal gradients. In other words, it matters whether foliage is dense or sparse, and whether it is concentrated higher in the canopy, lower in the canopy, or evenly distributed throughout.

## Implications [ & future research directions?]

*Elsa: If emphsaize future research directions, could move the remote sensing opportunities to this section and frame modeling section around opportunities to use models to further explore open questions, scale these findings in space and time, and influence predictions* *(In this section, we consider implications of the patterns reviewed above for our understanding of the future of forests–both how we model them and what sorts of responses we can expect under climate change.)*

Still, partitioning into its constituent components, let alone vertically partitioning transpiration rates in the canopy, remains a challenge. Eddy covariance techniques, sap flow measurements, and stable isotope analysis offer useful tools, although errors can be large (Williams et al 2004, Herbst et al. 1996). To date, empirical analyses of ET vertical partitioning and interactions with temperature and vegetation structure have be concentrated in midlatitude ecosystems (e.g. Haverd et al 2009, 2011, Staudt et al. 2011, Ringgaard et al. 2014) *(KAT: but see Kunert et al. 2017 -not sure if this is equivalent)*. With respect to changing temperatures, the net effect of leaf- and plant-level thermal responses remains an active area of research, including both how vertical variation in thermal sensitivity influences forest ecosystem dynamics and biosphere-atmosphere interactions.

Having established how physical conditions and biological form and function vary across vertical gradients, we now turn attention to the implications of these patterns for our understanding of how forest ecosystems may be impacted by global change, and our ability to project this across space and time.

## Global change responses

### canopy disturbance

Canopy structural composition and largely influence understory species composition and soil fertility (Majasalmi & Rautiainen, 2020), buffering capacity, which in-turn is influenced by the hydrological cycle (**???**). Each of these are subjected to change through climate-driven disturbances such as drought, deforestation, fire and related disruptions (Senf *et al.*, 2018). Frequent drought-related hydraulic limitation in forests alters species thermoregulation (Sastry *et al.*, 2018), and decreases tree canopy circumference (Aussenac, 2000). With larger trees suffering disproportionally greater hydraulic stress during drought, can contribute to increasing larger tree mortality in forests around the world (**???**; Brienen et al. 2015; Bennett *et al.*, 2015; Stovall *et al.*, 2019). Increases in loss of canopy cover (Senf *et al.*, 2018; Senf & Seidl, 2020), or increase in mortality of big trees (e.g. Senf *et al.* (2018)) would increase canopy roughness, also associated with reduced canopy structural complexity, altering microclimates with local heating effects and surface energy balance components (Stark *et al.*, 2020; Zellweger *et al.*, 2020).

Increasing global temperatures can increase canopy sometimes above ambient temperature when transpiration is low, leading to temperate and tropical forest canopies functioning beyond or close to their optimal photosynthetic threshold (Mau *et al.*, 2018a; Huang *et al.*, 2019). Temperature driven photosynthesis limitation is reducing tree growth rates, accompanying a global trend towards more frequently disturbed forests dominated by younger trees (McDowell *et al.*, 2020). 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). Each of these changes have potential feedbacks to climate change.

### warming

While forest microclimates are insulated from macroclimatic extremes, they are still subjected to warming trends (Maes *et al.*, 2020; Bertrand *et al.*, 2020). Understories experience a distinct set of pressures as microclimatic warming combines with conditions of limited light and related foliar traits, inter-species resource competition, and herbivory (Bartholomew *et al.*, 2020; Niinemets, 2010). Since temperature sensitivity is directly linked with plant metabolic processes and performance, even around 1 degree of warming can lead to changes in plant species composition and growth (Bertrand *et al.*, 2011, 2020). Plant communities in forest microclimates are already undergoing thermophilization (**???**; **???**; Zellweger *et al.*, 2019, 2020) with increasing threat to microclimatic fauna (Scheffers *et al.*, 2013) . Tree-ring analysis in mesic temperate forests shows reduced growth of understory trees relative to overstory with warming temperatures (Rollinson *et al.*, p. 2020). Whereas warming in other cases is associated with taller understory trees with lower LMA that complete their lifecycle in the understory, under closed-canopy temperate forests (Maes *et al.*, 2020). Evidence shows that warming and heat waves can also drastically alter canopy and understory phenology and forest photosynthesis (Zohner & Renner, 2019).

Additionally, warming will disproportionately affect the less warm-adapted functional types within the forest canopy, essentially creating holes in the canopy that will take a long time to refill (especially in slow-growing tropical sub-canopy specialists), as is observed with Andean thermophilization (death is faster than recruitment and growth). Differential mortality within the canopy structure will alter the profile of metabolism and hence emergent forest function. Such alteration to canopy structure may be detectable by lidar and thermal remote sensing. If we know how metabolism maps to the thermal profile, then the observed forest structural changes can inform prediction of forest function.

## Scaling across space and time

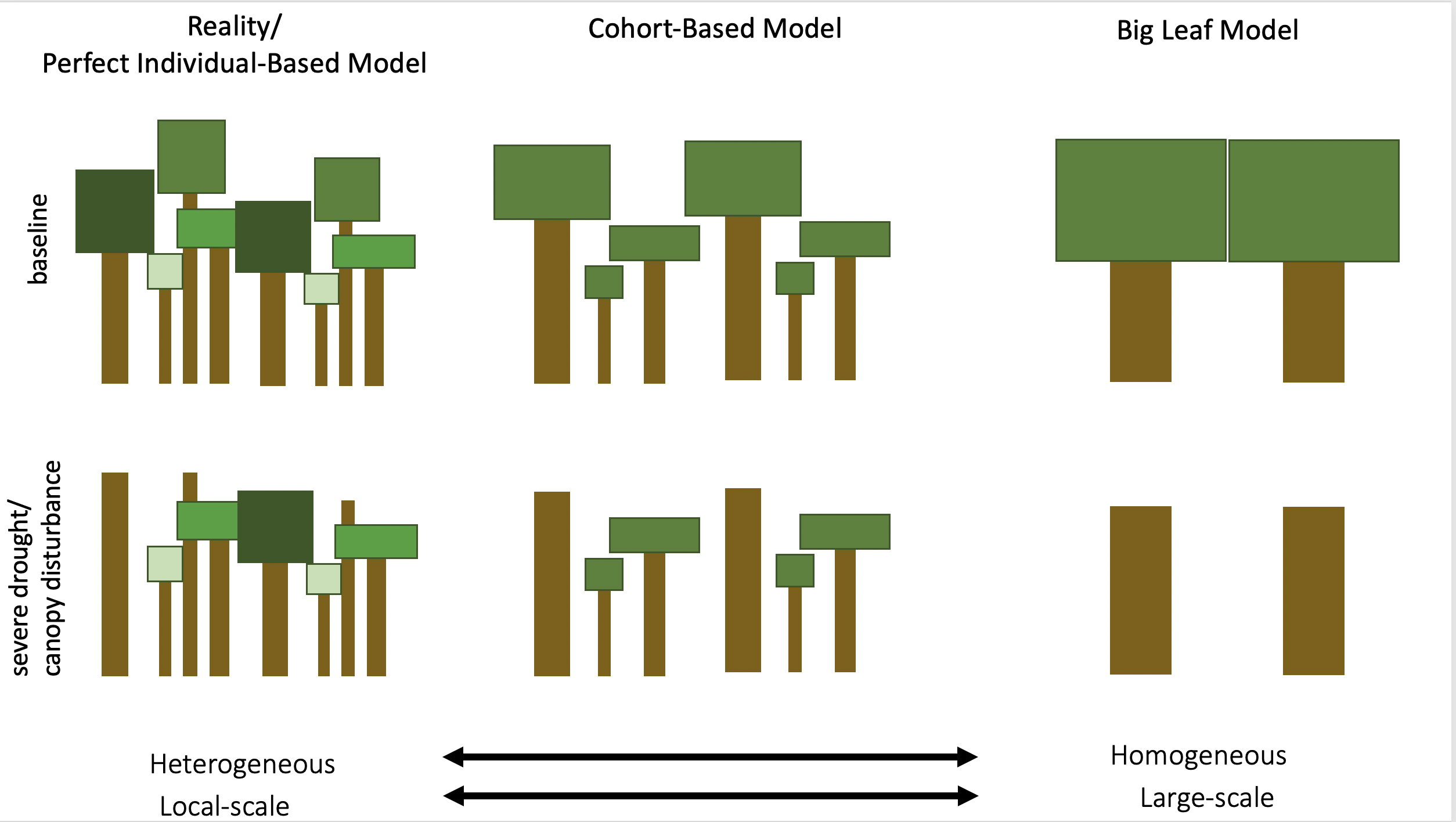
*Scaling our understanding across space and time requires remote sensing and models.*

### Remote sensing

An increasing availability of airborne and spaceborne LiDAR remote sensing data offers a promising opportunity for mapping vertical thermal gradients and vegetation structure. [Drone based FLIR cams, tower thermal cams (Pau et al 2018), ECOSTRESS]. To evaluate large-scale ecosystem patterns, high resolution vertically resolved vegetation structure from LiDAR data can be analyzed in combination with collocated field measurements collected using towers (FluxNet REF), canopy cranes (Nakamura *et al.* (2017)), or by tree climbing (REF – e.g. Asner papers, Shenkin et al – Unding Jami’s work). Existing research efforts have already revealed incredibly heterogeneity in vegetation structure, diversity, traits, and properties both within and across ecosystems (REFS – Stovall, Schneider, …others).

### Representing Vertical Gradients in Models

Models are needed to predict future ecosystem dynamics, which remain one of the largest sources of uncertainty in Earth System Model (ESM) projections of the future of global carbon cycling and climate change (*Friedlingstein et al. 2006*). Dynamic global vegetation models (DGVMs) comprise the land surface models in ESMs used to predict the global distribution of vegetation types and biosphere-atmosphere feedbacks (Cao & Woodward, 1998; Foley et al., 1996; Sitch et al., 2003; Woodward & Lomas, 2004). DGVMs operate at a range of scales and have varying degrees of complexity, ranging from detailed individual-based models (*a.k.a.* forest gap models), which represent vegetation at the level of individual plants, capturing spatial variability in the light environment and microclimates at high vertical and horizontal resolution (Christoffersen et al., 2016; Fischer et al., 2016; Fyllas et al., 2014; Sato et al. 2007; Shuman et al. 2014; Smith et al., 2001; Bugmann, 2001; Dietze & Latimer, 2011), to big-leaf models that reduce 3D vegetation structure across the entire biosphere into a single vegetation layer (Fig. 5). This simplification results in greater computational efficiency and thus easier integration into ESMs (Arora & Boer, 2010; Bonan et al. 2003; Cox, 2001; Krinner et al., 2005), although it comes at a cost of a lack of representation of important demographic processes, canopy gap formation, vertical light competition, competitive exclusion, and successional recovery from disturbance (Feeley et al., 2007; Hurtt et al. 1998; Moorcroft et al., 2001; Smith et al. 2001; Stark et al., 2012). Improved representation of vegetation demographic processes in ESMs, specifically including forest canopy architectural variation in both horizontal and vertical directions, has repeatedly been identified as a critical step toward reduced uncertainty and more accurate characterization of biologically mediated feedbacks (Banerjee & Linn 2018, Evans, 2012; Moorcroft, 2006; Moorcroft, Hurtt, & Pacala, 2001; Purves & Pacala, 2008; Thomas, Brookshire, & Gerber, 2015). Still, as models increase in complexity, model developments and improvements have direct tradeoffs with increased computational cost and potentially decreased interpretability of model output, highlighting the need to identify and parsimoniously represent the most essential drivers of forest ecosystem function.



**Figure 5. DRAFT. Enrich this by showing 3-4 carefully selected scenarios (e.g., baseline, warming-mesic, warming-drought, canopy disturbance), and maybe a few key processes/ consequences (leaf T, C balance).** [Issue #42](https://github.com/EcoClimLab/vertical-thermal-review/issues/42).

**The findings of this review reinforce the notion that representing vertical structuring is essential to capturing forest dynamics under global change.** *[how?]*

**The computationally feasible approach to representing vertical structuring in DVGMs lies in Cohort-based models (CBMs), which sit in the middle of this continuum between the oversimplified vegetation dynamics in big-leaf models and the computational expense of individual-based models.** CBMs represent vegetation as cohorts of individual plants, grouped together based on properties including size, age, and functional type (Haverd et al., 2013; Hurtt et al., 1998; Lischke et al. 2006; Medvigy et al. 2009; Moorcroft et al., 2001; Scherstjanoi et al. 2014; Smith et al., 2014; Weng et al., 2015). *(KAT: I think all of the following content is great, but probably needs to be heavily tightened:)*

To review the vertical light environment and thermodynamics of CBMs in more detail, we focus here on the Ecosystem Demography model version 2 (ED2), a model that is actively undergoing continued development and application across a range of ecosystems and landscapes (Moorcroft et al. 2001, Longo et al 2019 Pt 1 & pt 2). ED2 is also the progenitor of the Functionally Assembled Terrestrial Ecosystem Simulator (FATES), the DGVM coupled with the Energy Exascale Earth System Model (E3SM) (Xu & Christoffersen 2017 ) . In ED2, cohorts are tracked across multiple size-classes or individuals within the same plant functional type (PFT). Each cohort can encounter multiple light environments within a single climatic grid cell depending on patch-level disturbance history and vertical light competition that modulates interactions between plant traits and resource acquisition. Heterogeneity in the light environment and canopy structure across patches within a grid cell gives rise to varying horizontal and vertical micro-environments that differ in temperature, humidity, soil moisture, and soil nutrient conditions (Fisher et al 2018). The energy, water, and carbon dioxide cycles are solved separately for each patch in ED2, while fluxes and storage associated with individual plants are solved for each cohort within patches (Longo et al 2019). As a result, vegetation structure and functional distributions are emergent properties in the model that depend on plant functional traits and their interactions with abiotic environmental conditions. Each plant perceives a unique environment, including incident light, temperature, and vapor pressure deficit that varies across local scales in association with the horizontal and vertical position of each cohort relative to other cohorts, in addition to patch level differences in topographic and edaphic conditions. Coexistence of different vegetation types emerges from different environmental niches, either along a successional gradient of light availability or vertical position in the canopy (Moorcroft et al., 2001; Smith et al., 2001; Purves & Pacala, 2008).

Temperature is an atmospheric boundary condition driving the ED2 model (Longo et al 2019). Each patch in each grid cell is defined by a thermodynamic envelope, comprised of distinct thermodynamic systems for each soil layer, temporary surface water or snow layer, the aboveground component of each cohort, and the canopy air space (Longo et al 2019). The atmosphere above and outside of the canopy air space is referred to as free air and is determined directly from boundary conditions in ED2. Patches exchange heat and mass with the free air and lose water and associated energy through surface and sub-surface runoff. The net enthalpy flux of soil, temporary surface water, and vegetation thermodynamic systems in ED2 are exclusively due to associated water fluxes, whereas the eddy flux between the free air and the canopy air space includes both water transport and flux associated with the mixing of air with different temperatures between the canopy air space and free air (Longo et al 2019).

Because most CBMs are spatially implicit within grid cells, direct and diffuse photosynthetically active radiation (PAR) is distributed to cohorts of differing heights using radiative transfer models that depend on designated rules associated with how crown architecture is represented, rather than via direct spatial competition determined by spatially explicit crown locations (Fisher et al. 2010?). The flat-top crown method used in ED and ED2 stacks cohort-layers vertically, and a radiative transfer model is used to determine radiation absorbed by each layer at its midpoint, meaning that each cohort is shaded by all taller cohorts. This is distinct from other models that represent crown architecture using a perfect plasticity approximation (PPA) approach, which assumes that tree crowns completely fill canopy gaps through phototropism (stem leaning) and crown filling (Strigul et al. 2008). Discrete canopy layers are comprised of self-organizing crowns that all receive the same incoming radiation. Once the canopy layer is filled with tree crowns, successive shorter trees inhabit the subsequent understory layer and are shaded by the trees in the canopy (Fisher et al 2010/2018?). Models using the PPA approach differ in number of understory layers (e.g. some only have one) (Fisher et al 2018). Though an improvement over big-leaf models, models that separate the canopy into only two layers (e.g., sunlit and shaded portions) 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. (E.g. see de Pury & Farquhar, 1997).

## Conclusions

* across vertical gradients, directional trends in biophysical environment and leaf traits are the rule, suggesting that the physiology and ecology that have these as their underpinnings should also vary
* a number of studies confirm that this is the case.
* However, when we ask the critical question of how the temperature sensitivities of metabolism and woody growth varies across these different environments, we can’t say much– there are only a small number of studies, often showing insignificant differences or mixed results.
* We lean towards the conclusion that while large canopy trees ware the most vulnerable to warming when combined with drought, understory trees may be more vulnerable under more mesic conditions, but more research is needed.
* Critically, change to the vertical gradient–e.g., through increased mortality of canopy trees–will change processses across forest strata, with potentially dramatic consequences. (some of the literature on forest degredation or fragmentation could inform what happens when those gradients change)

## SI files

Appendix S1. Methods for NEON vertical profiles

Appendix S2. Methods for leaf energy balance modeling

Appendix S3. Methods for literature review

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