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

**Authors (so far, not necessarily in final order):** Nidhi Vinod1, Martijn Slot2, Ian McGregor3, Elsa M. Ordway4, Marielle N. Smith5, Tyeen Taylor, Lawren Sack, Kristina J. Anderson-Teixeira1,2\*

**Author Affiliations:**

1. Conservation Ecology Center; Smithsonian Conservation Biology Institute; Front Royal, VA 22630, USA
2. Smithsonian Tropical Research Institute; Panama, Republic of Panama
3. Center for Geospatial Analytics; North Carolina State University; Raleigh, NC 27607, USA
4. Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA 02138, USA
5. Department of Forestry, Michigan State University, East Lansing, MI 48824, USA

\*corresponding author: [teixeirak@si.edu](mailto:teixeirak@si.edu); +1 540 635 6546

## 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).

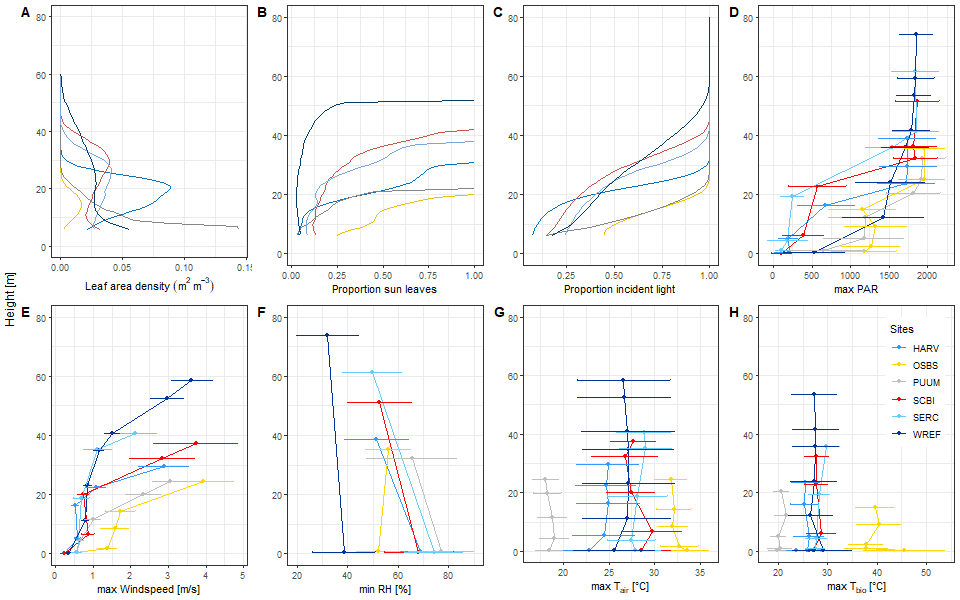
# Review of vertical gradients

## 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. Foliage LAI and density mediate light regime, where denser upper canopies exposed to greater PAR values limit light to canopy interiors, lower canopy layers, and the understory. This light gradient is more pronounced under broadleaf forests than needleleaf forests (Fig. 2; Lowman & Rinker, 1995; Aussenac, 2000; von Arx *et al.*, 2012; Poorter *et al.*, 2019b).

The amount of light reaching lower canopy, understories and forest floors are highly variable, ranging from high light gaps to deeply shaded understory regions (Chazdon & Fetcher, 1984; Smith *et al.*, 2019; Tymen *et al.*, 2017). Forest floors of tropical forests with densely packed overstory trees, receive approximately 1-2% of the incident light that hits the top of the canopy (Chazdon & Fetcher, 1984; Roberts *et al.*, 1990; Parker *et al.*, 2019), whereas mixed-wood boreal and northern temperate forest floors receive around 4-5% of full sunlight (Bartemucci *et al.*, 2006)and needle-leaf forest floors receive 17-34% of incoming sunlight (Baldocchi *et al.*, 1997). Small canopy gaps and wind-induced movement of canopy leaves and branches also contribute light in the form sunflecks–around 10-80% of of photon flux density– to shaded forest regions that receive 1/3 of their carbon during photosynthesis through these short light 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).

These light regimes shape foliage at a vertical gradient, which in turn shapes the microenvironment. At a foliar level, resulting light-adaptation in the form of sun and shade leaf dichotomy also facilitates plant-adaptation to the light environment in the understory and the overstory, ultimately contributing to shaping the microenvironment, forest vertical-profile’s thermal sensitivity and their response to warming [Fauset *et al.* (2018); Miller *et al.* (2021); Michaletz *et al.* (2015); *De Frenne et al. 2021*]

### 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. Understory wind-speed is also substantially reduced with increased canopy height (Jucker *et al.*, 2018). Consistent with these results from NEON sites, higher wind speeds at greater heights within a forest canopy 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 varies with foliage characteristics mentioned above, and water availability (Davis *et al.*, 2019). Diurnally, tropical, temperate broadleaf, mixed-conifer and non-pine conifer forests offset temperatures positively and negatively where they maintain cooler, lower maximum temperature and vapor pressure deficit () in the daytime, and warmer higher minimum temperature during nighttime in the understory respectively, relatively more than pine and boreal forests, and nearby clearings [von Arx *et al.* (2012), *Defrenne et al. 2021*; (**???**); Zellweger *et al.* (2019); Rambo and North, 2009]. Similarly, when compared to neighboring tree crop agricultural plantations, intact tropical forests maintain lower understory peak daytime and , attesting to increased buffering with LAI and canopy cover (Jucker *et al.*, 2018; Hardwick *et al.*, 2015). On the other hand, open-forests with sparse stands, have lower buffering capacity with greater vertical air mixing, greater light permeability through canopy layers and sometimes greater soil heating (Rambo & North, 2009). Therefore, they maintain higher daytime maximum temperature and light availability in the understory that are closer to nearby clearings (Martin *et al.*, 1999; Rambo & North, 2009; von Arx *et al.*, 2012; De Frenne *et al.*, 2019). During the night, pine forests can maintain warmer understory temperatures than above canopy, due to long wave infrared radiation from the soil caused by daytime solar warming (von Arx *et al.*, 2012).

Buffering is also affected by canopy roughness, turbulent air flow and the canopy boundary layer. As a result, taller trees upto 20m in an old-growth Borneo forest (which coincided with forests of higher LAI) have shown to lower mean and max of VPD and temperature in the understory. However, beyond a certain tree height, temperature and VPD offset plateaud (Jucker *et al.*, 2018; Hardwick *et al.*, 2015).

Seasonally, the capacity to moderate buffering is greater with water availability. During the wet season, tropical forests in Panama (Rey-Sánchez *et al.*, 2016), temperate forests in Switzerland (von Arx *et al.*, 2012) and coastal forests in Brazil (Fauset *et al.*, 2018, Tymen et al. 2017), have all shown to offset temperatures positively in the understory, with lower maximum air temperatures and higher relative humidity below canopies and understories than above forest canopies and gaps. However, during the dry season of a semi-deciduous tropical forest in Panama, maximum temperatures were similar in the upper and lower canopy, partially because in the dry season some canopy trees are leafless, resulting in more light reaching the sub-canopy, and more boundary layer turbulence (Rey-Sánchez *et al.*, 2016). Similar results were observed in a temperate deciduous forest in the eastern United States (McGregor *et al.*).

Under colder conditions, minimum [] is also buffered by forest canopies, increasing negetive temperature offset in the understory. Across Europe [Zellweger *et al.* (2019); *Defrenne et al. 2021*] and in the northwestern United States (**???**) higher minimum temperatures under forest canopies have been observed relative to nearby clearings. Greater radiative heat loss in exposed areas results in lower . 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.)*

### Humidity and evaporative demand

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

Along with temperature, forest canopies moderate relative humidity (RH) in below-canopy microclimates, which tends to decrease with increasing maximum temperature. In three European forests (Broadleaved, Non-Pine Conifer, Pine), canopy buffering decreased daily maximum and increased daily minimum RH in below-canopy microclimate compared to a nearby open area. RH moderating capacity was stronger under broadleaved and non-pine conifer forests than pine, and greater in wetter conditions, and in summer and autumn months than winter (von Arx *et al.*, 2012).

RH, in combination with temperature, determines vapor pressure deficit (), an important metric expressing the driving force of water loss from a leaf. Atlantic forests in Brazil during the wet season tend to have higher , and in the upper canopy and canopy gaps than in the understory where and tend to be lower (Fauset *et al.*, 2018; Tymen *et al.*, 2017). This means that canopy leaves tend to be exposed to higher *evaporative demand*, higher stomatal constraints (Niinemets & Valladares, 2004).

### 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

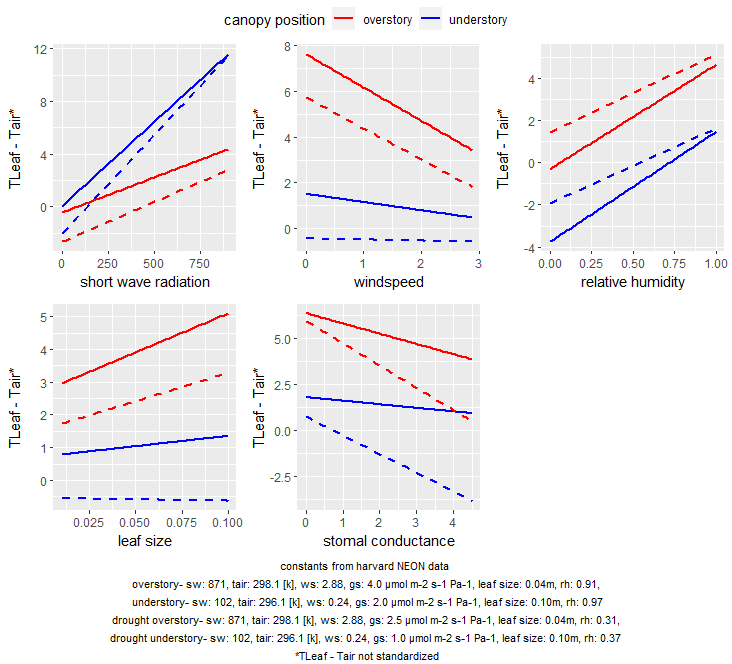
With higher altitude, forest light environment varies along with plant growth habits, therefore shapes microclimate conditions. In Switzerland forests, buffering capacity has shown to be stronger in low altitude forests than high altitude forests (von Arx *et al.*, 2012), partly because trees in these high-altitude forests are sparserly distributed (von Arx *et al.*, 2012) or have open canopies with greater light interception through canopy layers (Rajsnerová *et al.*, 2015). Less capacity to buffer climatic conditions in open, high altitude forests might have implications to forest regeneration and climate change (Fauset *et al.*, 2018; von Arx *et al.*, 2012). This is also observed in timberline and temperate humid-mountain forests in China, where tree height decreased with altitude, and tree growth sensitivity (based on tree-rings) increased (Liang *et al.*, 2019).

The strength of buffering also varies with respect to distance to the coast, topographic position, elevation (Zellweger *et al.*, 2019). Riparian forests tend to sustain buffering, protecting understory temperatures even during increasing temperature extremes compared to open areas by a stream (Davis *et al.*, 2019; Macek *et al.*, 2019)

## Leaf temperature

### Biophysical drivers

**Many of the vertical gradient biophysical and trait variables reviewed above affect leaf temperature, , which in turn has a strong influence on leaf metabolism (see following section).** Leaves adapt to their biophysical environment. Maintaining optimum leaf temperature for metabolic optima in relation to their biophysical environment maximizes carbon assimilation in a given circumstance. This is done through the adaptation of leaf traits to the surrounding biophysical environment (Perez & Feeley, 2020; Michaletz *et al.*, 2015). Thus, 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). When leaves are cooler than air at high temperature and warmer than air at low temperature, they considered to exhibit limited homeothermy. When leaves are drastically warmer than such as sometimes in the upper canopy, this is considered megathermy. In some cases, can be equalled to , showing poikiolothermic behavior (Cavaleri, 2020; Drake *et al.*, 2020).



**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).

**(paragraph on radiation as a driver)** Incoming solar radiation is a strong driver of leaf temperature, relative to , such that even at low maximum , leaves exposed to high radiation loads can experience elevated , greater than . On the other hand, under conditions of constant radiation and water availability, evaporative cooling sustains under increased (Cavaleri, 2020).

Greater upper canopy wind speeds (Fig. 2) result in higher boundary layer conductance () for canopy leaves, which increases linearly with wind velocity (Daudet *et al.*, 1999). Large to heat transfer, in turn, results in a smaller difference between and . In low wind conditions, because to heat transfer is comparatively small, can become substantially elevated in relation to under high radiation (Leigh *et al.*, 2017; Martin *et al.*, 1999). Additionally, the thickness of the air layer is proportional to boundary layer resistance at the surface of the leaf through which water vapor diffuses after leaving the stomata. This tends to be greater in the understory than in the canopy (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)** Leaf thermoregulation is a tradeoff between water use strategy and optimum leaf temperature, which is influenced by stomtal conductance that facilitates heat dissapation and leaf water content that affects the rate of leaf warming (**???**; Fauset *et al.*, 2018). Leaves with open stomata can maintain similar to at high radiation loads, *with coolest leaves at intermediate sizes (~10mm)*. Under hot conditions, leaves exposed to higher wind speeds would be most effective at cooling when sufficient water is available to maintain high stomatal conductance [Drake et al. 2018]. However, during the midday, can become highly elevated above when or is low. This is caused by increase in air temperature and VPD driving greater leaf water demand than water transport, which limits stomatal conductance along with decreased leaf water content, therefore limiting heat dissapation (**???**; Fauset *et al.*, 2018). On the other hand, buffered leaves should tend to maintain cooler daytime leaf temperatures for any given level of stomatal conductance.

**In addition, leaf size and morphology, which vary dramatically across the vertical gradient (reviewed in following section), impact and therefore leaf temperature.** \*Smaller leaves have higher to heat transfer, allowing them to dissipate heat more efficiently than larger leaves (Leigh *et al.*, 2017; Bauerle & Bowden, 2011).  
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 (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).

### 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, as well vertical biophysical gradient, affect vertical distribution of leaf temperature. While the high-light environment of the upper canopy would tend to dramatically increase above , particularly under low-wind conditions, strong vertical gradients in leaf morphology and sometimes *evapotranspiration* have a counteractive effect, such that vertical trends in are much less pronounced than would be expected based on the physical setting alone.

Particularly, in open forests with sparse distribution of trees and lower buffering capacity, as observed in needle-leaf forests, lower canopy can be substantially warmer than upper canopy , reflecting microclimate conditions of either increased vertical air mixing or heating from the ground (Muller *et al.*, 2021), light permeating through canopy layers and low wind velocity or still air in the lower canopy compared to the upper canopy (Hadley & Smith, 1987; Martin *et al.*, 1999; Zweifel *et al.*, 2002; Muller *et al.*, 2021). Greater heat stress and in the lower canopy is also observed in open Australian desert trees (Curtis *et al.*, 2019) and among timberline krummholz needle-leaf trees, both growing close to the ground (Hadley & Smith, 1987), this is analogous to greenhouse effect caused under dense lower canopies. Similarly, in dry conditions, in a semi-decidudous tropical moist forest in Panama where some trees loss canopy leaves, sun leaves can be cooled relative to more than lower canopy shade leaves (Rey-Sánchez *et al.*, 2016). In other tropical dry conditions, inner canopy can be warmer than above canopy and air temperature due to conditions of greater relative humidity (Dietz *et al.*, 2007). Under other conditions tracks and therefore differs little between understory and canopy (Fig. 2).

At night when solar radiation is not a factor, differences in across the vertical gradient are very modest; for instance, Bolstad *et al.* (1999) observed similar nighttime ’s in the canopy and understory of a temperate broadleaf forest.

**However, canopy leaves can reach much higher maximum , and higher , than understory leaves.** Especially in closed-canopy forests with increased buffering capacity, large leaf to air temperature differences and high leaf temperatures are found in the upper canopies compared to lower canopies, caused by midday stomatal closure that reduces transpirational cooling [Slot et al. 2019]. This is seen in Atlantic, Brazil forests (Fauset *et al.*, 2018), Puerto Rico tropical wet, moist and subtropical wet forest(Mau *et al.*, 2018b; Miller *et al.*, 2021), semi-deciduous tropical forest during the wet season in Panama (Rey-Sánchez *et al.*, 2016), and as well in a temperate forest (Mau *et al.*, 2018b).

In three forest types- US temperate deciduous, Puerto Rico tropical wet and tropical moist, exceeded temperature optimum for photosynthesis in the upper canopies of all three forests, with increasing - with height. - was observed to be greatest in temperate deciduous forest compared to tropical moist and wet. Greater light input in exposed upper canopy leaves can sometimes elevate leaf temperature above air temperature, making upper canopy leaves susceptible to heat stress, more than scattered light in lower shaded leaves (Doughty & Goulden, 2008; Mau *et al.*, 2018b)

## Leaf traits

**Leaf thermoregulation largely depends on leaf traits. Leaf traits co-vary with their environment (Michaletz *et al.*, 2016), shaped by the intensity and availability of light and water demand, in order to optimize C uptake, thermoregulate and balance metabolism, across forest vertical strata, and thus show different degrees foliar plasticity (Zwieniecki *et al.*, 2004; Michaletz *et al.*, 2015)**

#### *(clarify light vs height - 1 paragraph)*

Leaf morphological adaptation to the local microenvironement takes place during leaf expansion (Zwieniecki *et al.*, 2004). Degrees of direct to diffused light and consequental 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, exposed sun leaves are typically smaller in size and width, thicker, hairier and have greater lobation, and buffer biophysical conditions for shade leaves. Whereas shade leaves adapt to diffused light and stable microenvironment through investing in light capture efficiency by expanding specific leaf area (SLA) (Zwieniecki *et al.*, 2004; Rozendaal *et al.*, 2006; Mathur *et al.*, 2018). Respective leaf traits also play a role in heat dissapation where exposed sun leaves are more efficient in dissapting heat than buffered shade leaves (VOGEL, 1970).

Particularly in dense forests, the upper, outer canopy leaves of taller trees are exposed to dramatically different biophysical conditions than leaves in the canopy interior or understory (Figs. 2, S1-S#). Leaf traits are critical to maintaining desirable and, in turn, shaping leaf metabolism (following section) and carbon balance. It is unsuprising, then, that leaf traits vary dramatically across vertical gradients.

While light based acclimation in leaf traits is well established, research on solely height-based leaf trait variation is sparse due to the difficulty of isolating increased tree height from light. 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.However, the majority of relevant research has focused on exposure gradients near ground level, with by far the most common study type being comparisons of sun and shade leaves. While light is the primary axis along which leaf traits vary, both theory and empirical evidence indicate that other factors–for example, height on a tree or exposure to evaporative demand (Fig. 2)– are 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*). Under constant light conditions (photon flux density), increase in height (>35m) showed decrease in canopy stomatal conductance, along with increasing (Schäfer *et al.*, 2000; Ambrose *et al.*, 2010). Adaptations to increasing height and hydraulic contraints show that leaf size [Kaare H. Jensen and Maciej A. Zwieniecki, 2013] and lobation (Kusi & Karsai, 2020) tend to decrease, whereas leaf mass per area (at greater than 20m) tends 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 form and function remains an important area for research, but is beyond the scope of the current review. For the purposes of interpreting the results presented here, we note that patterns across light and height gradients age generally similar, at least in direction (Table 1), but likely to be modified by covarying biophysical constraints.

*(The following notes need to be condensed/ worked into the paragraph above or discussion of specific traits. No need to get very specific (listing species studied, traits)–what we want is generalization. The goal is to answer the question, “Do we expect light gradients to be equivalent to height gradients, or is there variation attributable to height that is not captured by light gradients?”)*

#### *(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-individuals exposed canopies substanially buffer inner and lower canopies from light and biophysical conditions. Thus leaf traits in canopy positions vary accordingly (Casas *et al.*, 2011). Several studies point towards common variations in leaf anatomical, structural and biochemical trait plasticity at a vertical intra-canopy gradient across individual trees (Sack *et al.*, 2006; Niinemets *et al.*, 2015a; Chen *et al.*, 2020). The differences among these traits contribute to leaf temperature distribution across the gradient (Fauset *et al.*, 2018; Michaletz *et al.*, 2016) Table 1 summarizes relevant traits for thermal sensitivity.

Additionally, 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 characterize trait relationships and leaf responses through the whole vertical canopy (Keenan & Niinemets, 2016), such as by incorporating sun and shade in modelling leaf economic spectrum (LES) traits within-canopy gradient, partly because LES theory was developed using mainly sun exposed (upper canopy) leaves (Chen *et al.*, 2020).

*(Krista: the above paragraaph is really interesting, and I like the idea of starting off the section by mentioning what controls the formation of leaf traits. However, I think it gets into more detail than needed. Also, is there work out there on how they’re influenced by temperature/ water at the time of formation? I’d broaden to include the full microenviroment (without increasing length)*)



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

#### Morphological traits

Along the vertical gradient, exposed leaves are better equipped to dissapate heat than shaded leaves, through adaptive traits such as smaller leaf size, leaf dissections–lobes and serration– decrease effective leaf width and therefore increase the rate of heat convection per unit area between leaf and air. (Schuepp, 1993; Sack *et al.*, 2006; Leigh *et al.*, 2017; VOGEL, 1970). Mechanisms such vertical leaf angles and temporary wilting reduce surface light exposure and lower leaf temperature in exposed canopies (Ishida et al. 1999; Niinemets, 1998). Hydraulic traits, for example leaf vein and stomtal density, also help maintain a balance photosynthesis and thermoregulation, in the high light environment of exposed canopies [Brodribb et al. 2010]. On the other hand, leaf temperature increases with effective leaf width and leaf size (Fauset *et al.*, 2018), along with thermal time constant that is longer due to the increase in boundary layer thickness and stomatal resistance, and lower convective cooling (Leigh *et al.*, 2017; Wright et al. 2019; Fauset *et al.*, 2018). Therefore, shade leaves that typically have greater leaf size and effective leaf width compared to sun leaves, remain cooler in buffered conditions but can become substanially warmer under greater light or (Leigh *et al.*, 2017). Additionally, understory leaves tend to open their stomata wider (stomatal apeture) than upper canopy leaves (Kosugi & Matsuo, 2006).

#### Biochemical and physiological traits

Canopy nitrogen distribution along the vertical gradient optimizes to prevent photoinhition for sun leaves during direct light and shade leaves during sunflecks, and could mediate sun vs. shade leaf response to heatflecks under available soil nitrogen conditions (Kitao *et al.*, 2018). Therefore, during growing season, nitrogen per area [], along with LMA, leaf soluble sugars, starch and non-structural carbons increase with height and light, typically greater in exposed canopy positions or sun leaves compared to shade [Coble & Cavaleri (2014); Coble *et al.* (2016); Weerasinghe et al. 2014]. Phosphorous per area follows a similar trend along the canopy gradient, but with increased growth at higher light P uptake, in some cases, cannot keep up and thus shows variable results (Poorter *et al.*, 2019a)

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

Proportional to vertical light gradients at an intra- and inter-species level, sun exposed leaves have greater pools of xanthophyll pigments, comprised of violaxanthin, antheraxanthin and zeaxanthin [] than in shaded leaves. []–an antioxidant scavenging function–protects against cellular damage by converting excess light into heat energy dissipation through non photochemical quenching of excitation energy, enabling short-term acclimation to high temperature and light (Niinemets *et al.*, 1998; Mathur *et al.*, 2018).

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

##### *Leaf lifespan* [Elsa: phenology more broadly? - leaf lifespan, fruiting, flowering links to temperature and thermal gradients?]

*Leaf lifespan generally increases with LMA. LMA and leaflifespan is greater with available light, and largely depends on the cost of carbon investment in a leaf, which varies across species sun vs. shade leaves [****double check****] 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*

*Among species that can be deciduous, greater proportion of deciduous individuals in larger size classes (Condit et al. 2000).*  *Spring and fall leaf phenology in temperate deciduous forests (Augsburger).*

### Interspecific varaiation

Across tree-size ontogeny, canopy and understory trees of same species in tropical, temperate, and conifer forests show fundamental light adapted leaf traits in their biophysical environment, as observed and similar to within-species gradient (Thomas & Winner, 2002; Rozendaal *et al.*, 2006; Houter & Pons, 2012). Isolating ontogeny, under constant light conditions of open-grown canopy and understory trees, for example in large gaps, differences in traits showed significantly greater LMA, photosynthetic capcity per area, and stomatal conductance in taller canopy trees compared to saplings (Thomas & Winner, 2002; Houter & Pons, 2012). Across multi-species canopy and understory, while fundamental adaptations to light and water are observed, their pasticity to light differs along with inherent traits such as leaf shape, size and width, stomtal conductance levels and therefore influence leaf temperatures.As a result, some species might be more susceptible to heat stress at a vertical gradient than others (Fauset *et al.*, 2018).

*from Martijn in Tleaves figure: One thing that might be more relevant in tropical than in seasonal temperate forests, is the issue I mentioned before about the difference between shade leaves of canopy trees and leaves of understory species. The understory species in the tropics (the ones that won’t necessarily make it to the canopy, and can reproduce in the understory) appear to invest more in leaf longevity than in light harvesting per se, so even though they are in the shade, they do not have large leaves with low LMA. This would be a deviation on, or a special case of, the understory parameters you are using now. I don’t think we necessarily need to incorporate that in this figure, but I think it would be useful to be able to say that for understory species with small, high LMA leaves the effects of windspeed, radiation, RH, etc, are greater/smaller than for the understory species parameters in the figure. DOes this make sense? Is this relevant at all for seasonal forests? The only thing that comes to mind is Ilex, but maybe there are other species?*

*(KAT: a lot of this content should probably move up the the intro to this section)*

##### Isoprene production

* Isoprene production *capability* as a trait

## 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 sun leaves are equipped to thermoregulate more efficiently than shaded leaves, they are largely constrained by stomatal conductance; and therefore their ability to photosynthesize as well. During the day, max transpiration rate and stomtal conductance 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 occurs when evaporative demand exceeds water transport capacity in exposed leaves thereby increasing (Zwieniecki *et al.*, 2004; Sanches *et al.*, 2010). Thus, stomatal limitation is greater and steeper in exposed canopies than shaded leaves (Sanches *et al.*, 2010; Hernández *et al.*, 2020).

### Photosynthesis

**Photosynthesis is generally higher in sun leaves and 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).

Leaf temperature beyond photosynthetic optimum temperature declines photosynthesis [**REF**]. Photosynthesis has a peaked response to temperature, where 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 leaf temperature (e.g. Slot & Winter (2017); Smith et al. 2020 [temperate/boreal refs needed) and eventually due to biochemical constraints (refs. e.g. Sage & Kubien 2007; Varhammer et al. 2015 ).

Photosynthesis will also be affected by heat stress, when photoinhibition reduces photosynthesis either as a result of photoprotective; non-photochemical quenching or related to irreversible leaf damage leading to leaf necrosis. At increasing temperatures, photosynthetic system II [PSII] is particularly vulnerable. Damage to PSII can lead to decreased electron transport rates and photosynthetic failure. Irreversible damage to PSII is done at 40-60C (Baker 2008; Feeley *et al.*, 2020). 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.*, 2015a)

*[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 [agreed. Again the importance of differentiating between within-species and among species trait variation. Also; steepness of the vertical gradient in light and VPD. In very tall trees a gradient in water potential might cause a gradient in stomatal limitations of net photosynthesis]*

**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!*), as optimum temperature for has shown to increase 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 found for of and (Slot *et al.*, 2019; Hernández *et al.*, 2020),as well in vertical species profile in Puerto Rico forests, no trend in the optimum temperature for net photosynthesis was found (Mau *et al.*, 2018a; Miller *et al.*, 2021), and no significant trend in 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.*

*(KAT: let’s cut the portion on T50 down to one or at most two par:)*

**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 thresholds 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].

Across forest species, typical values across latitude and climate are ~45-50C (O’ sullivan et al. 2017). and decreases with elevation, as seen in tropical forests in Panama and Columbia and across latitudes (O’sullivan *et al.*, 2017; Feeley *et al.*, 2020; Slot *et al.*, 2020) and varies with 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, observed through 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 margins. Rather, in across species sun leaves, higher photosynthetic heat tolerance experienced higher maximum leaf temperatures, and showed low optimum temperature for C assimilation [] and therefore had narrower breadth of thermal safety margins (difference between maximum leaf temperature and ) (Perez & Feeley, 2020)

**Thermal tolerance (e.g., ) varies with exposure, but there are no studies isolating effect of height.** Thermal tolerance and have been predominantly measured on sun leaves; thus there remains limited information on leaves with varying light exposures and vertical height gradient.

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

In other cases, leaf thermal tolerance reflects microclimatic stress along a vertical gradient. For *Acacia Papyrocarpa* (Benth.) trees in an arid region of southern Australia, higher composite climate stress and thus was observed in the lower north-facing canopy position compared to other canopy positions. Greater in lower north-position also correlated with longer leaf thermal time constants, along with with low-wind speed and greater canopy and air temperature (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 sun leaves (Chen et al. 2020), but its temperature sensitivity appears to be similar between between sun and shade leaves.**

While respiration tends to increase along the vertical gradient, with greater respiration in canopy leaves [Bolstad *et al.* (1999); Weerasinghe et al.2014], temperature sensitivity of respiration––shows conflicting findings with no definite trend.

In two forests, north-eastern oak dominated-deciduous forest in the US and conifer-dominated temperate New Zealand rainforest, across species was found to be greater in upper-canopy leaves than in lower-canopy leaves, where values differed between species (Turnbull *et al.*, 2003). Similarly, in sweetgum (*Liquidambara styraciflua*), upper canopy sun leaves showed greater than lower within-canopy shade leaves (Harley *et al.*, 1996). However, in other feild studies, didnot vary across species vertical profiles and light exposure such as in a lowland tropical Australian forest study (Weerasinghe *et al.*, 2014), and across temperate trees at Coweeta (Bolstad *et al.*, 1999) . 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*). Bolstad *et al.* (1999) found evidence of acclimation, but there remained a declining trend of respiration with elevation.

With temperature increase, foliage photosynthesis and respiration are coupled at different rates upto photosynthetic thermal optimum. Beyond this inflection point, fluxnet global data analysis shows that photosynthesis declines whereas respiration increases exponentially, therefore, moving from carbon sink to carbon source with increasing temperature, 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 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; however regardless of light, isoprene emission increases with T such as in understory shaded leaves?

## 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.** 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?)*

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.

On the basis of phenology, temperate understory trees tend to leaf out earlier than canopy due to ontogenetic variation in tree size rather than biophysical conditions [Vitasse et al. 2013], and, increase in annual temperatures has shown to have implications on understory phenology, relative to canopy trees [Zohnner and Renner, 2019]. However, short-term May spring heat waves have shown to negetively impact partially-expanded canopy leaves by inducing leaf shedding and decreasing photosynthesis in reflushed leaves, more than in 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, increased exposure to light increases non structural carbon reserve (NSC), plant height, foliage robustness, while also increasing evapotranspiration, decreasing hydraulic conductivity, increasing chances of photoinhibition in leaves should water availability become limited, however with available water overall sensitivity to stress decreases. Understory shaded/younger trees have comparatively less NSC reserve due to light limitation as a primary stressor [which differs among shade-tolerant/intolerant], decreased plant biomass, increased leaf biomass, and decreased evapotranpiration demands, as well as greater investment in light harvesting than in photosynthesis–with greater overall sensitivity to stress and reduced tolerance. Larger NSC reserves in trees with greater light and water availability allows them to tolerate greater number of stressors compared to understory/younger trees that are able to tolerate only a fewer stressors making them overall more sensitive to stress [such as temperature]. Thus, overall stress sensitivity decreases and tolerance increases with increasing height, light and age.(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*

Interaction between degrees of shade x ontogeny with rising temperature needs more scientific attention because a huge part of understory vegetation lies within variations of light and shade spatio-temporal gradient.



\*\*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

*(this section is currently just a bunch of text moved from elsewhere/ loose notes)*

### warming

* Influence of increasing temperatures on species compositions and feedbacks to future forest microclimates and function?

*Frequent drought-related hydraulic limitation in forests alters species thermoregulation (Sastry et al., 2018), and also decreases tree canopy circumference (Aussenac, 2000) due to sensitivity of overstory trees to variability in water availability and precipitation (Rollinson et al., p. 2020). Larger trees suffer disproportionally greater hydraulic stress during drought [resulting in heat stressed canopy-leaves], which may contribute to increasing larger tree mortality in forests around the world should frequencies of drought continue to increase (McDowell et al., 2008; 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) are 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). However, in mesic forest conditions, availability of soil water enables canopies with suitable foliar traits to remain cool through continuous evapotranspiration even during increasing air temperature, thereby buffering understory microclimates, unless relative humidity is so high as to reduce rate of evapotranspiration (Perez & Feeley, 2018).*

*While forest microclimates are insulated from macroclimatic extremes, they are still subjected to warming trends (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). Tree-ring analysis in mesic temperate forests shows reduced growth of understory trees relative to overstory with warming temperatures (Rollinson et al., p. 2020). In addition, understory growth phenology is more sensitive to warming than canopy– showing earlier spring onset and later autumn senescense (Zohner & Renner, 2019).*

*The capacity of buffering largely depends on canopy cover and water availability (****???****), each of which is subjected to change through climate-driven disturbances such as drought, deforestation, fire and related disruptions (Senf et al., 2018). Increasing global temperatures can increase canopy leaf temperatures 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). In wetter conditions, available water facilitates leaf transpiration through open stomata; however increased relative humidity in tropical regions indirectly caused by increased temperature reduces transpiration, leading to high leaf temperatures in the canopy (Tibbitts, 1979; Perez & Feeley, 2018).*

if we expect ‘shade’ plants to have a different sensitivity to climate change than sun leaves, the consequences of climate change for demography and species community composition of the forest will depend strongly on the category of shade plants being considered

*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.*

### canopy disturbance

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

*(there’s a lot of literature on canopy disturbance impacts–tap into that in this section)*

Microclimate warming has implications for forest regeneration (von Arx *et al.*, 2012). 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.

increases in mortality of big trees (e.g. Senf *et al.* (2018)) would increase canopy roughness

## Scaling across space and time

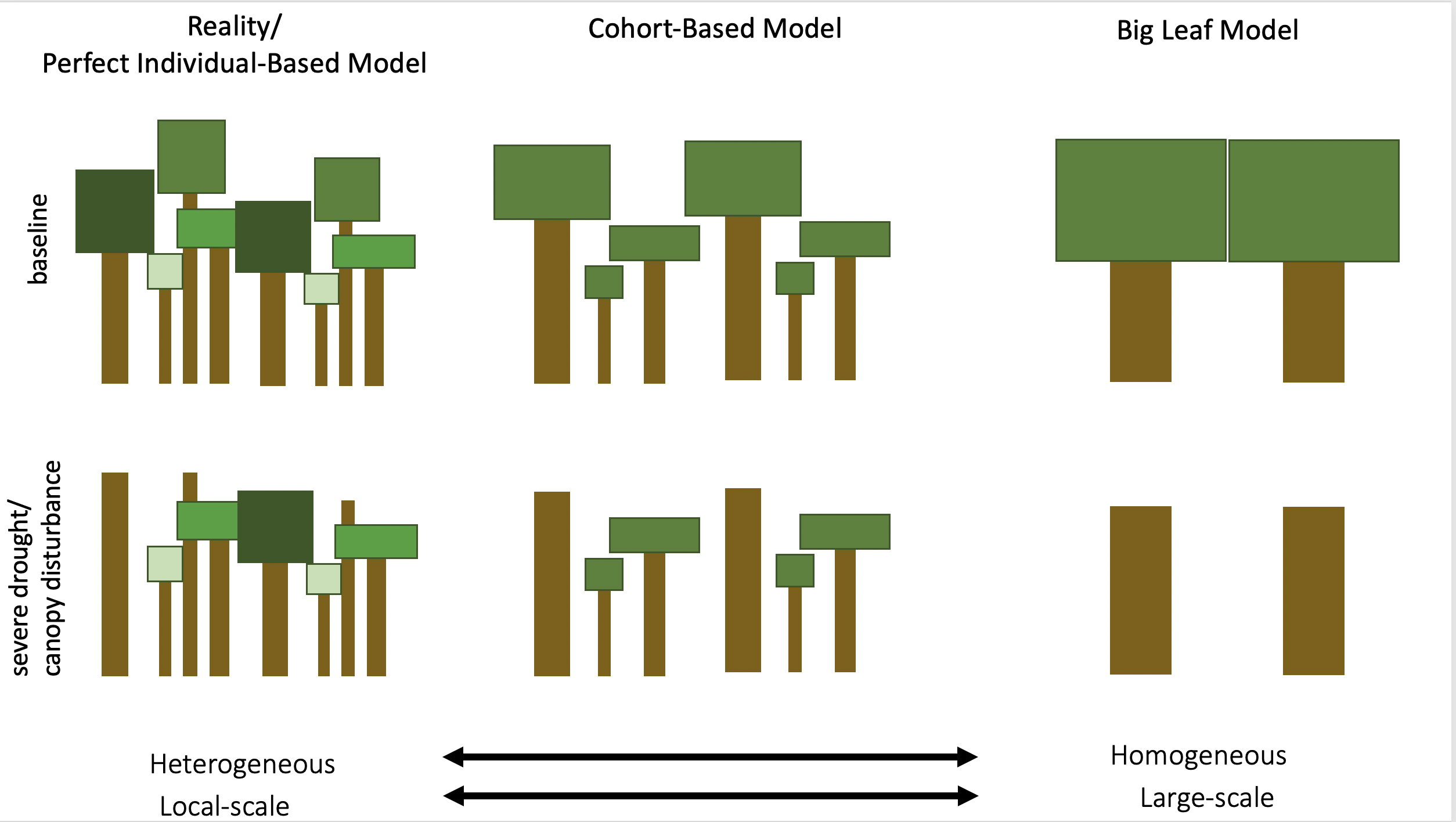
*Scaling our understanding across space and time requires remote sensing and models.*

### 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?]*

~~In general, DGVMs range from Individual Based Models (IBMs) on one end of the complexity and scale spectrum to big-leaf models on the other end. Most climate models incorporate vegetation dynamics using big-leaf models, which include many first generation DGVMs that reduce 3D vegetation structure across the entire biosphere into a single vegetation layer. 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). On the other end of the spectrum are IBMs, also referred to as forest gap models, representing vegetation at the level of individual plants (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). These models are often stochastic and spatially explicit, capturing spatial variability in the light environment and microclimates at high vertical and horizontal resolution. As a result, however, IBMs are computationally expensive and tend to be run at very local scales.~~

**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). ~~Although this cohort approach serves as a compromise that incurs lower computational costs than IBMs while capturing many of the same dynamics, CBMs do not incorporate the stochastic processes of IBMs that typically allow for greater representation of functional diversity (Fisher et al., 2010).~~

*(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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