**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.*). Leading to, individually or in combination, can 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 (Ozanne *et al.*, 2003; Nakamura *et al.*, 2017) 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 (Michaletz *et al.*, 2016; Fauset *et al.*, 2018). 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. (2004a) 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 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, acts as the primary physical barrier between the atmosphere and the forest floor, buffering multiple aspects of the understory conditions and is critical in influencing–and is influenced by–the vertical biophysical gradient.(Fig. 2).**The distribution of this foliage is structured in correspondence with the size, and varies across tree structures and forests.  
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 ; Almeida *et al.*, 2016 ; Stark *et al.*, 2020). 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).

### 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 the vertical gradient of forests globally, amount of light decreases from canopy tops to the forest floor which is mediated by foliage LAI and density. This gradient is most pronounced under broad-leaf and mixed forests where light reaching forest floors, incident to the canopy-top range from ~1-2% to 4-5%, respectively [Fig. 2; Aussenac (2000); Smith et al., 2019; Tymen et al., 2017; Chazdon & Fetcher (1984); Parker *et al.* (2019); Bartemucci *et al.* (2006)] compared to needle-leaf forest floors that receive ~17-34% (Baldocchi *et al.*, 1997). Sunflecks, are another axis of light for shaded forest regions, caused by small canopy gaps and wind-induced canopy movements (Way & Pearcy, 2012). 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, and in closed-canopy forests (McGregor *et al.*; **barnardSeasonalVariationCanopy2016a?**) to open savannas (Curtis *et al.*, 2019) wind speeds increase with height. With daily maximum wind speeds averaging up to **#** $m s^-1^$ higher at the top of the NEON vertical profile than at the bottom

### 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), *Defrenne et al. 2021*; (**davis\_microclimatic\_2019?**); Zellweger *et al.* (2019); Rambo & North (2009); Martin *et al.* (1999)] and neighboring tree crop agricultural plantations (Hardwick *et al.*, 2015; Jucker *et al.*, 2018).

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

### 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 vapor pressure deficit [], 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; Tymen *et al.*, 2017; Fauset *et al.*, 2018). Increased tree height [upto 20m with higher LAI] can to lower mean and max temperature and in the understory. Beyond a certain tree-height, the offset can plateau (Hardwick *et al.*, 2015; Jucker *et al.*, 2018).

### Carbon dioxide

**Atmospheric 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

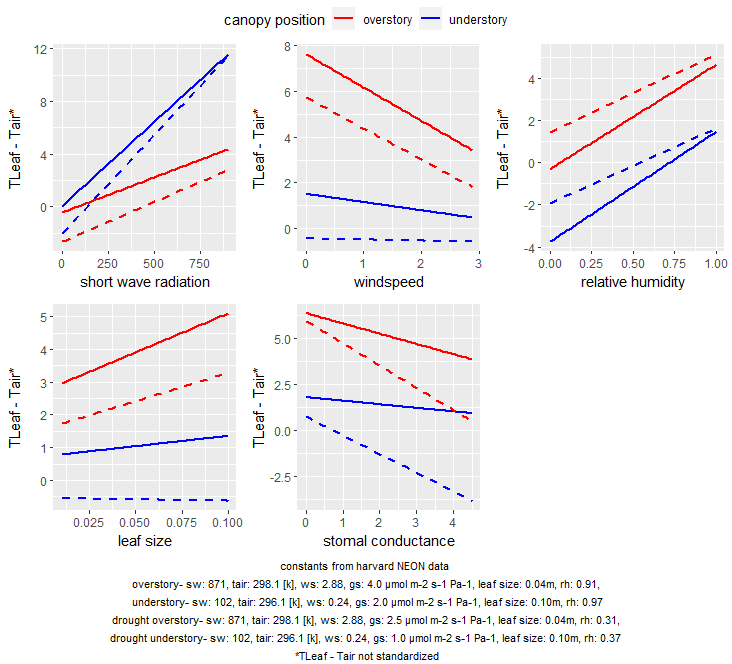
With altitude, the strength of buffering decreases, moving to open-forests (von Arx *et al.*, 2012; Rajsnerová *et al.*, 2015; Liang *et al.*, 2019; Zellweger *et al.*, 2019), greater in wetter than drier regions [**REF**] and increases with proximity to water, for eg. in riparian forests. (Davis *et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

## Leaf temperature

### Biophysical drivers

**Vertical biophysical drivers reviewed above influence heat and water stress patterns, and leaf temperature distribution along the vertical gradient, which in turn shapes leaf metabolism (see following section).** Along the biophysical dynamics vertically, leaves adjust to their environment by maintaining optimum , for carbon assimilation and metabolic processes (Michaletz *et al.*, 2015; Perez & Feeley, 2020). Therefore, 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).

is determined by the energy balance of a leaf and can be estimated based on basic biophysical principles (Campbell & Norman, 1998; Michaletz *et al.*, 2016; Muir, 2019) (Fig. 3) where - is 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).

This balance is a tradeoff between water use strategy and optimum (Koch *et al.*, 1994; Fauset *et al.*, 2018) such that, because stomatal conductance () facilitates heat dissipation, when water demand exceeds water transport, driven by irradiance,, or drought, conservation of water ( limitation) occurs at the cost of increasing .

Therefore, while under maximum , leaves can maintain similar to at high solar-radiation loads until light saturation, during limitation solar radiation can drastically elevate above (Cavaleri, 2020).

High wind speed (Fig. 2) decreases - due to large boundary layer conductance () (Daudet *et al.*, 1999). Therefore, under hot conditions, high wind speeds and high would enable cooling [Drake et al. 2018] but at lower wind conditions, thickness of air layer at the leaf surface curbs rapid leaf-to-air heat transfer, through smaller , which increases - (Roberts *et al.*, 1990; Martin *et al.*, 1999; Stokes *et al.*, 2006; Leigh *et al.*, 2017)

**(paragraph on hydraulics as a driver of leaf T:e.g., water on leaves - evaporative cooling - and leaf water content)** Inherent leaf is an important factor for which is typically greater across species exposed sun-leaves due to stomata density than shade leaves. However, because factors driving limitation–irradiance, VPD and –increase with exposure, limitation is steeper for sun- than shade-leaves, driving an increase in (Leigh *et al.* (2017); Fauset *et al.* (2018)). On the other hand, shade leaves can remain cooler under buffered conditions, but lower leaf can result in greater under slight heat stress.

**In addition, leaf size and morphology, which vary dramatically across the vertical gradient (reviewed in following section), impact and therefore leaf temperature.** Small leaves tend to heat and cool faster due to higher , maintaining lower - than large leaves that take longer to heat and cool due to low (Bauerle & Bowden, 2011; Leigh *et al.*, 2017).

### In-situ observations

**The principles outlined above, vertical microclimate profile (Fig. 2), leaf traits (see following section), and evapotranspiration (where is this discussed? and do we say anything about evaporation?) together shape in-situ observations (Fig. 3).**

Particularly, in open-forests with lower buffering capacity, lower-canopy is greater than upper canopy, due to vertical air mixing, greater light permeability, still air in the lower canopy and heating from the ground can collectively increase (Hadley & Smith, 1987; Martin *et al.*, 1999; Zweifel *et al.*, 2002; Rey-Sánchez *et al.*, 2016; 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 closed-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 from limitation, than buffered lower-canopies (Doughty & Goulden, 2008; Rey-Sánchez *et al.*, 2016; Fauset *et al.*, 2018; 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 highly 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 is controlled by leaf traits, that are in-turn adapted to their environment (Michaletz *et al.*, 2016). Therefore, are critical in maintaining desirable and shaping leaf metabolism (following section) across forest vertical strata (Figs. 2, S1-S#)(Zwieniecki *et al.*, 2004; Michaletz *et al.*, 2015)**

Leaf morphology adapts to the local microenvironment during leaf expansion (Zwieniecki *et al.*, 2004) where 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). This dichotomy in leaves is observed along the vertical gradient where canopy-leaves vary dramatically from canopy-interior and understory due to the differences in biophysical conditions (Figs. 2, S1-S#). But at greater tree height, biological–tree-height–and biophysical–light, temperature, and evaporative demand (Fig. 2)–also play a role in shaping leaf 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 show that, canopy decreases 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).

However, disentangling tree-height related biological and biophysical drivers (Fig. 2) on leaf traits remains an important area for research, which is sparse, but is beyond the scope of the current review. Here, our primary interest is in how leaf traits and function vary across the vertical gradient from the canopy-top to the understory in forests. 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 gradients 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] vertical dynamics (Michaletz *et al.*, 2016; Fauset *et al.*, 2018) where Table 1 summarizes relevant traits for thermal sensitivity. The characterization of trait relationships and responses through the vertical canopy is a strong research need because LES theory was developed using mainly sun exposed (upper canopy) leaves (Keenan & Niinemets, 2016; Chen *et al.*, 2020).



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

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| nocite: | |
| Mau *et al.* (2018a); (**cobleLightDrivesVertical2014?**); Sack *et al.* (2006); Chin & Sillett (2017); Wyka *et al.* (2012); Atherton *et al.* (2017); Kenzo *et al.* (2015); Kusi & Karsai (2020); Dang *et al.* (1997);Gebauer *et al.* (2015); Marenco *et al.* (2017); Kafuti *et al.* (2020); (**vanwittenbergheVariabilityStomatalConductance2012?**); Zhang *et al.* (2012); Weerasinghe *et al.* (2014); Oldham *et al.* (2010); Ichie *et al.* (2016); Gregoriou *et al.* (2007); Levizou *et al.* (2005); Liakoura *et al.* (1997); Fauset *et al.* (2018); Niinemets *et al.* (1998); Ishida et al. 1999; Millen & Clendon (1979); Smith & Carter (1988); Hadley & Smith (1987); Panditharathna *et al.* (2008); Baltzer & Thomas (2005); Dietz *et al.* (2007); Coble *et al.* (2016a); Scartazza *et al.* (2016); Duursma & Marshall (2006); Harley *et al.* (1996); Hernández *et al.* (2020); Turnbull *et al.* (2003); Chen *et al.* (2020); van de Weg *et al.* (2012); Cavaleri *et al.* (2008); Königer *et al.* (1995);Matsubara *et al.* (2009); Harris and Medina 2013; Hansen *et al.* (2002); Poorter *et al.* (1995); Coble *et al.* (2016b); Niinemets *et al.* (2004b); Poorter *et al.* (2000) |

#### Morphological traits

Exposed-canopy leaves are better adapted to heat and water stress than shaded-leaves where sun-leaves are often thicker, smaller, hairier, with greater leaf dissections (VOGEL, 1970; Sack *et al.*, 2006; Leigh *et al.*, 2017), hydraulically efficient [Brodribb et al. 2010], with adaptive strategies such as leaf-angle and rolling (Niinemets, 1998). All, collectively regulate -photosynthetic balance.On the other hand, shaded leaves invest more in light capture than in heat dissipation, with lower convective cooling [(**fauset\_differencsunes\_2018?**); Leigh *et al.* (2017); Wright et al. 2019]. Under homogeneous light conditions, sun-leaves in different canopy orientations are shaped based on and stress (Mediavilla *et al.*, 2019).

#### Biochemical and physiological traits

The distribution of biochemical traits enable photosynthesis and metabolic processes, and protect against heat and light damage in sun-leaves. , that is typically greater in the direction of new leaf growth (Niinemets, 2007), optimizes to prevent photoinhition in sun- and, shade-leaves during sunflecks, under available soil nitrogen (Kitao *et al.*, 2018).Similarly, carotenoids and xanthophyll pigments-violaxanthin, antheraxanthin and zeaxanthin [], an antioxidant scavenging and photoprotective function- convert excess light to heat dissaptation (Niinemets *et al.*, 1998; Mathur *et al.*, 2018). Constraints to biochemical traits, particularly can curb temperature acclimation (Kumarathunge *et al.*, 2019). Additionally, isoprene producing species are particularly advantageous in that it facilitates high heat tolerance in canopy positions[*REF*]

### Interspecific variation

Across forest species widely, show fundamental trait adaptation to light gradients similar to within-canopy traits (Thomas & Winner, 2002; Rozendaal *et al.*, 2006; Houter & Pons, 2012). However, between multi-species canopy and understory, trait plasticity to similar biophysical gradients can vary several-folds due to inherent specie-specific traits. Spatio-temporal gradients offer another axis for trait variation, as they are heterogenous in time and space [Ishii and Asano, 2007]. Across ontogeny of the same species in canopy and understory, traits such as LMA, photosynthetic capacity [per area] and increase with height, separate from light (Thomas & Winner, 2002; Houter & Pons, 2012). Therefore, while general patterns of thermoregulation can be observed across species, some might be more suspectable to heat stress at a vertical gradient than others (Fauset *et al.*, 2018).

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

##### *Leaf lifespan*

New-leaf growth along the light gradient constantly shades leaves underneath. Therefore, exposed-canopies have greater proportion of young leaves than shaded regions that have older leaves. Acclimation to shade from sun-exposure, and vice-versa, is more possible in younger leaves that are devoloping traits than in mature leaves where traits have been developed. In such cases, change in light can result in dropping of leaves [Niinemetes, 2007]. *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. Indeed, greater proportion of deciduous species are found in drier tropicaal regions than wetter, and among species individuals that can be deciduous, greater proportion are in larger size classes than understory species that are seldom deciduous (**conditQuantifyingDeciduousnessTropical2000b?**). Therefore, deciduous leaf-loss can influence biophysical gradient and (Rey-Sánchez *et al.*, 2016). Spatio-temporal leaf-emergence in deciduous-temperate forests also shapes biophysical gradient where leaf-emergence is delayed with height-ontogeny with understory species leafing-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 mediates crucial leaf-atmosphere interaction across species, exposed-sun-leaves, though equipped to thermoregulate efficiently are largely constrained by than shade-leaves (Sanches *et al.*, 2010; Hernández *et al.*, 2020). Max transpiration rate and peaks in exposed-canopies during the day (Kosugi & Matsuo, 2006; Sanches *et al.*, 2010) and declines through midday and afternoon due to stomtal closure (Zwieniecki *et al.*, 2004; Sanches *et al.*, 2010; **kochDiurnalPatternsLeaf1994b?**).

### 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)].

**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 in an upper canopy leaf compared to shaded lower canopy leaf (Niinemets & Valladares, 2004). However, such a trend is not apparent among recent studies that 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).

**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].

**Thermal tolerance (e.g., ) sparsely varies with exposure among recent studies, but there are no studies isolating effect of height.**

150 years ago, Sachs studied garden species , though, with little information on shade-leaves [*REF*]. In 1994, Knapp et al. 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 Panama tropical forest, the results weren’t significant, with both measured near ground level.

in *Acacia Papyrocarpa* (Benth.) trees in an arid region was observed to reflect microclimatic stress index along a vertical gradient where lower north-facing canopy showed higher composite climate stress and greater than other canopy positions, that correlated with low wind-speed greater and longer leaf thermal time constants (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\*

*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.*

Recent studies show that while leaf thermal tolerances across species reflects local microenvironmental conditions than regional macroclimate, [Feeley *et al.* (2020); Slot et al. 2020; Perez and Feely 2020a] does not vary with phylogeny [Slot et al. 2020; Perez and Feeley 2020a].

Global s across latitude and climate range from ~45-50C (O’ sullivan et al. 2017). and , decrease with elevation in tropical forests and across latitudes (O’sullivan *et al.*, 2017; Feeley *et al.*, 2020; Slot *et al.*, 2020), vary with species (Krause *et al.*, 2010) and leaf traits (Sastry et al. 2018, Zhang *et al.*, 2012; Slot *et al.*, 2020). is also recently found to be greater in species with large leaves, and slow heating and cooling time [higher thermal time constant] whereas is found to be greater among species’ leaves with greater construction costs–greater LMA–compared to species with low LMA (Slot *et al.*, 2020). Perez & Feeley (2020) also found that, across species sun leaves that showed higher photosynthetic heat tolerance experienced higher , and showed low optimum temperature for C assimilation [] and therefore had a narrower breadth of thermal safety margins (-).

### 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 (Harley *et al.*, 1996; Turnbull *et al.*, 2003). In contrast, in a lowland tropical Australian forest study, did not vary across species vertical profiles (Weerasinghe *et al.*, 2014), similary across temperate trees at Coweeta though with a slight tendency to increase down the canopy relative to upper-canopy leaves as increased (*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].This can implication to canopies and gaps that reside at levels of greater . Whereas, greater can do the opposite, where it stifles evapotranspiration thereby increasing , particularly in tropical canopies where irradiance can have a greater effect [Fig.3; Perez & Feeley (2018); Tibbitts (1979)]. However, soil water loss during drought effects larger trees more than small trees because, limited soil-water cannot meet the evaporative demand via the long-distance water transport to the canonopy [Norway spruce study, bennett; McGregor *et al.*].

Additionally, understory growth can be 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 in temperate forests can negatively impact partially-expanded canopy leaves by more than understory saplings that are buffered, by inducing leaf shedding and decreasing photosynthesis [and C uptake?] in reflushed leaves [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. Interacting biophysical and biological stressors also show that stress sensitivity and ability to tolerate number of stressors increases with height, light and water. Partly because NSC reserves are greater in taller trees due to available light than in buffered trees that are light and NSC limited, therefore making buffered small trees more sensitive to stress (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

The complex interactions of the biophysical environment and biological–leaf traits, metabolic processes and distribution of trees–are highly interconneced, resulting in feedbacks to another. Therefore, climate-driven changes, such as rising temperature, can have implications to forests on several levels.

### canopy disturbance

Canopy buffering is crucial to microclimate functioning, which is influenced by hydrological-cycle at large [Davis et al. 2019]. Therefore, frequent droughts causes canopy disturbance, where less severe drought can decrease tree canopy circumference (Aussenac, 2000), and more severe droughts shows increasing larger tree mortality in forests globally [Senf *et al.* (2018); (**mcdowellMechanismsPlantSurvival2008?**); Brienen et al. 2015; Bennett *et al.* (2015); Stovall *et al.* (2019)]. Hydraulic limitation in forests can also alters species thermoregulation (Sastry *et al.*, 2018). Increasing temperatures shows increase in canopy above ambient temperature, and sometimes beyond or close to their optimal photosynthetic threshold (Mau *et al.*, 2018a; Huang *et al.*, 2019). Temperature driven photosynthesis limitation is also reducing tree growth rates, accompanying a global trend towards more frequently disturbed forests dominated by younger trees (McDowell *et al.*, 2020). Recent adavances in canopy studies further shows large loss of canopies in Europe caused by wind-induced disturbance and anthropogenic deforestation [Cornelius Senf, 2021; Senf *et al.* (2018); Senf & Seidl (2020)]. Loss of big trees (e.g.@senfCanopyMortalityHas2018a ) would increase canopy roughness, and reductions in canopy cover is associated with reduced canopy structural complexity and composition which changes understory species composition and soil fertility [*Majasalmi & Rautiainen (2020)*].Leading to altered biophysical gradient with local heating effects, (Stark *et al.*, 2020; Zellweger *et al.*, 2020), 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). 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 understory plant thermophilization (death is faster than recruitment and growth) (Zellweger *et al.*, 2019, 2020; **duqueThermophilizationAdultJuvenile2015a?**; **defrenneMicroclimateModeratesPlant2013?**) with increasing threat to fauna in microrefugias (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, in other cases warming 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). Heatwave and temperature can alter canopy and understory phenology, forest photosynthesis and forest C uptake (REFS, Zohner & Renner, 2019).

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

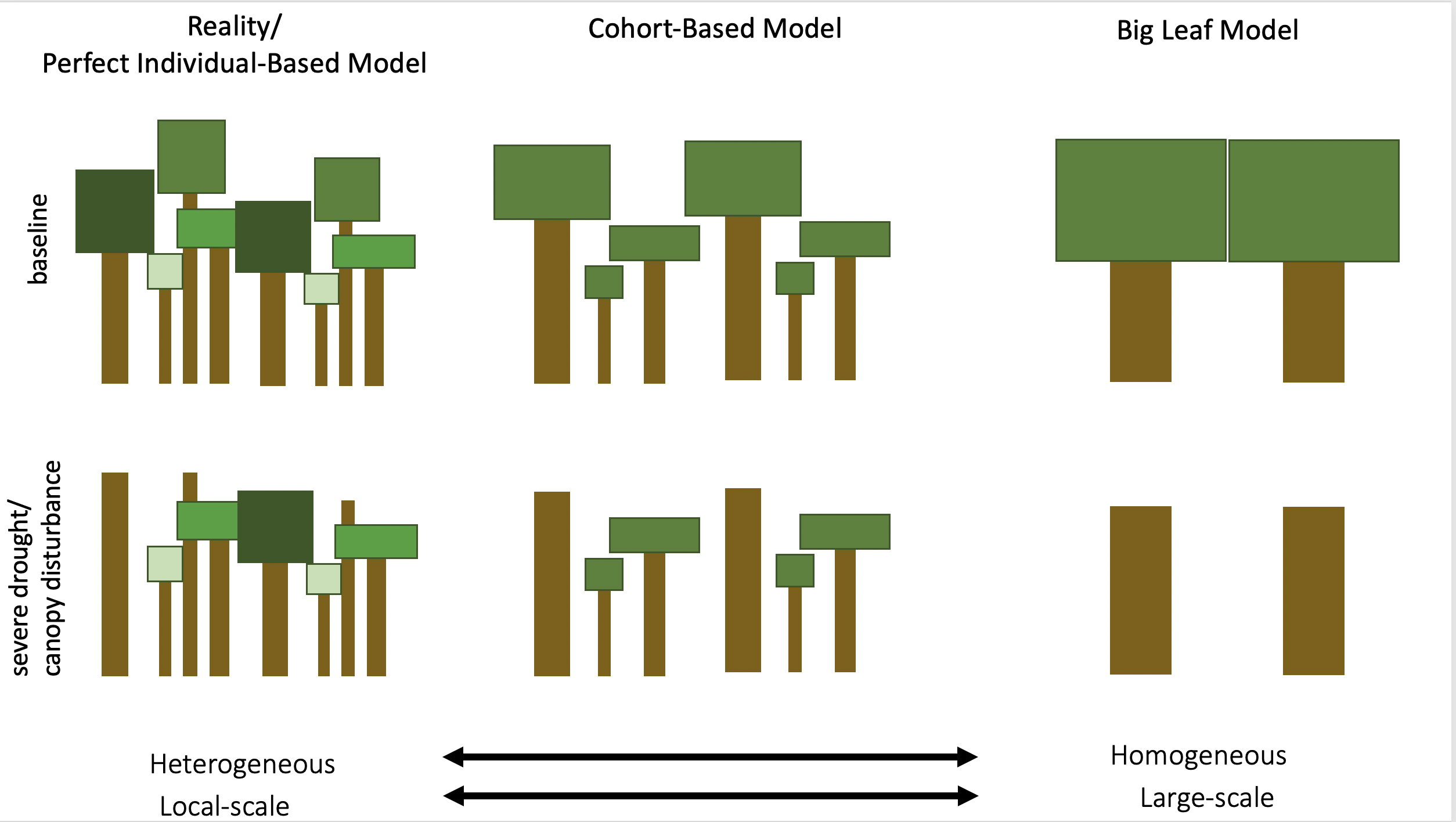
*Scaling our understanding across space and time requires remote sensing and models.*

### 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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