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

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

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19 **Summary**

20 Rising temperatures are influencing forests on many scales, with potentially strong
21 variation vertically across forest strata. Using published research and new analyses, we
22 evaluate how microclimate and leaf temperatures, traits, and gas exchange vary vertically
23 in forests, shaping tree ecology and ecosystem function. In forests with dense canopies,
24 upper-canopy leaves are exposed to the highest solar radiation and evaporative demand,
25 which can elevate leaf temperature (T_{leaf}), particularly when transpirational cooling is
26 curtailed by limited stomatal conductance. However, foliar traits also vary across height or
27 light gradients, partially mitigating the elevation of upper-canopy T_{leaf} . Leaf metabolism
28 generally increases with height across the vertical gradient, yet differences in thermal
29 sensitivity and damage thresholds across the gradient appear modest. Scaling up, tall trees
30 have higher absolute metabolic capacity and growth at both individual and ecosystem
31 levels, yet are disproportionately vulnerable to drought and damaging T_{leaf} 's, particularly
32 under climate change. In contrast, understory trees benefit from a buffered microclimate
33 but have fewer cooling mechanisms and thus may be disproportionately impacted under
34 hot, humid conditions, or when the buffering provided by large trees is lost. As the climate
35 changes, integrating the patterns and mechanisms reviewed here into models will be
36 critical to forecasting forest-climate feedbacks.

37 **Key words:** forest; vertical gradients; microclimate; leaf temperature; leaf traits; gas
38 exchange; ecosystem; climate change

39

I. Introduction

Forest responses and feedbacks to climate change will have a critical influence on the future of Earth's climate. Global average temperatures have risen 1.2 °C since 1900 (Rohde & Hausfather, 2020) and are expected to reach or even exceed +1.5 °C in the next 20 years (IPCC, 2021), accompanied by increasing severity and frequency of heat waves (IPCC, 2021; Meehl & Tebaldi, 2004) 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.*, 2021; Pörtner *et al.*, 2021) by altering rates of photosynthesis and respiration (Breshears *et al.*, 2021; Scafaro *et al.*, 2021; Corlett, 2011), causing foliar damage during heat waves (O'Sullivan *et al.*, 2017; Corlett, 2011), and reducing growth and elevating mortality during drought (Breshears *et al.*, 2021; McDowell *et al.*, 2020). The net result of higher temperatures may be increased or decreased tree growth and forest carbon sequestration, with decreases being more commonly documented across the world's forests (Oishi *et al.*, 2018; Sullivan *et al.*, 2020; Anderson-Teixeira *et al.*, 2021). The resulting feedbacks to the climate system, carbon storage, and changes in albedo and hydrology will in turn impact the future trajectory of climate change (Bonan, 2016), yet the degree of the impact remains uncertain (Krause *et al.*, 2018; Friedlingstein *et al.*, 2006).

A great measure of uncertainty arises due to the differential impacts of rising temperatures on trees of differential size and canopy position, especially as small understory trees exist in microenvironments that are substantially buffered by more exposed canopy trees (Davis *et al.*, 2019a; Zellweger *et al.*, 2019). Forests are vertically and horizontally stratified, with overstory canopies playing a crucial role in moderating forest climatic conditions (Nakamura *et al.*, 2017; Ozanne *et al.*, 2003), including buffering understory microclimates from extreme meteorological conditions (Zellweger *et al.*, 2019). This creates a vertical stratification of the biophysical environment such as temperature, light, wind, humidity and CO₂ concentrations 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 (but see Niinemets & Valladares, 2004). Importantly, this limits our ability to understand how warming temperatures will affect leaf-level metabolism, whole-plant performance, and, in turn, forest ecosystem dynamics, biodiversity, energy balance, ecosystem function, and biosphere-atmosphere interactions.

Here, we review how the biophysical environment and plant form and function vary across the vertical canopy gradient in forests. We focus on five key themes (Fig. 1): (1) the biophysical environment; (2) leaf temperature (T_{leaf}); (3) the leaf traits that most strongly influence T_{leaf} ; (4) leaf gas exchange (including stomatal and boundary layer conductance, photosynthesis, respiration, and volatile organic compound emission) and its thermal sensitivity; and (5) tree and ecosystem ecology. We then consider the implications for understanding forest responses to global change, including how these responses scale across space and time.

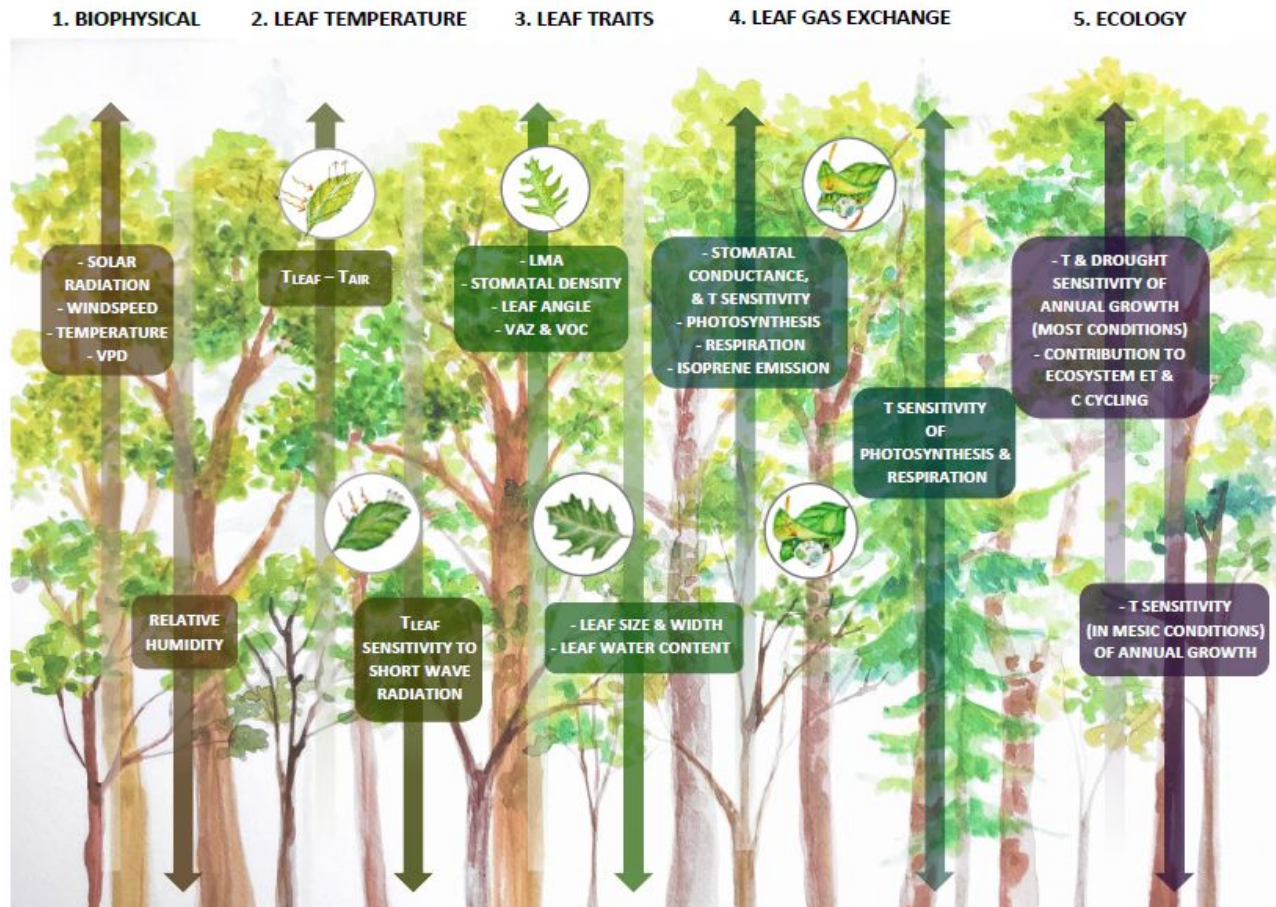


Figure 1. Schematic summarizing vertical gradients in forests according to (1) biophysical environment, (2) leaf temperature (T_{leaf}), (3) leaf traits, (4) leaf metabolism, and (5) tree and ecosystem ecology. Abbreviations are as follows: VPD: vapor pressure deficit; $T_{\text{leaf}} - T_{\text{air}}$: leaf-to-air temperature difference; LMA: leaf mass per area, VAZ: violaxanthin, antheraxanthin and zeaxanthin concentrations, VOC: volatile organic compounds; T sensitivity: temperature sensitivity; ET: evapotranspiration. Here, we summarize conditions in dense canopies during growing season and daytime conditions; patterns tend to be weaker, or sometimes reversed, in more open canopies, when canopy trees are seasonally deciduous, or at nighttime. Arrows indicate direction of increase, with double-pointed arrows indicating that observations have shown increases both higher and lower in the canopy.

II. Review of vertical gradients

1. The biophysical environment

The biophysical environment, defined here to include the physical structure of the vegetation and associated physical conditions, varies across the vertical gradient from the forest floor to the top of the canopy (Figs. 1, 2), with physical conditions in large part determined by the structure of the forest. 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 focal sites within the U.S. National Ecological Observatory Network (NEON; Fig. 2, Supporting Information Methods S1, Supporting Information Figure S1). While the focus here is on vertical gradients, it is important to note that in heterogeneous canopies with high gap fractions and large variation in tree height, or at forest edges, the biophysical environment can be more closely linked to the distance from the outer canopy than to height (Lowman & Rinker, 1995).

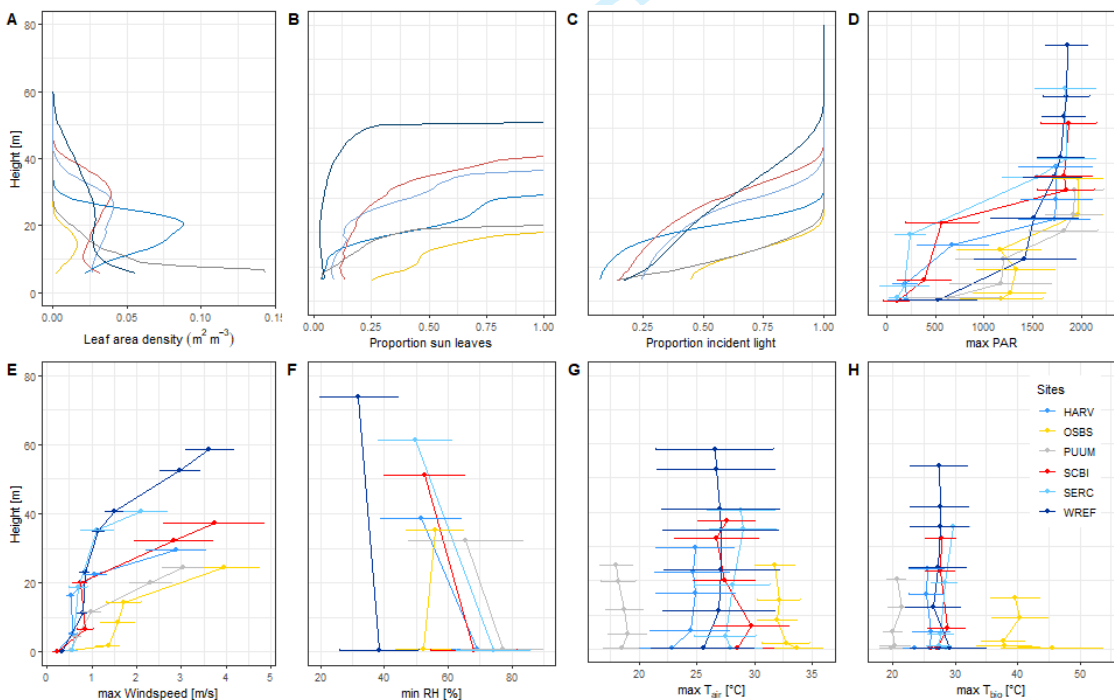


Figure 2. Vertical gradients in the biophysical environment for six US forest sites in the National Ecological Observatory Network (NEON). Height profiles are shown for: growing season (a) leaf area density, (b) proportion of sun leaves, and (c) proportion light incident to the top of the

canopy (as fraction relative to top of canopy), and for July mean \pm 1 standard deviation for (d) maximum photosynthetically active radiation (PAR), (e) maximum wind speed, (f) minimum humidity (min RH), (g) maximum air temperature (T_{air}), and (h) maximum biological temperature, (T_{bio}). Measurements extend from ground level (height = 0 m) to the top of the canopy (a-c, h) or above (d-g). Sites, which represent a variety of forest structures, include a mixed northern hardwood forest (Harvard Forest, MA; HARV), a subtropical longleaf pine savanna (Ordway-Swisher Biological Station, FL; OSBS), a tropical montane broadleaf evergreen forest (Pu'u Maka'ala Natural Area Reserve, Hawai'i; PUUM), two temperate broadleaf forests (Smithsonian Conservation Biology Institute, VA, SCBI; Smithsonian Environmental Research Center, MD, SERC), and a coniferous forest (Wind River Experimental Forests, WA; WREF). Further site information is given in Supporting Information Table S1, and analysis details in Supporting Information Methods S1. Vertical profiles in micrometeorological variables (d-h) at all six NEON sites are shown in Supporting Information Figure S1.

Canopy foliage acts as the primary physical barrier between the atmosphere and the forest floor, buffering multiple aspects of the understory conditions. It is critical in influencing – and is influenced by – the vertical biophysical gradient (Fig. 2). Leaf area density (*i.e.*, leaf area per unit volume) patterns along the vertical gradient are heterogeneous across forests (Fig. 2a-b, Supporting Information Figure S1). Tropical and temperate forests with dense canopies dominated by broadleaf trees generally have highest leaf area density in the upper canopy layers, but understory leaf area density is often relatively high in the understory as well, sometimes with undulating patterns (e.g., SCBI, SERC and HARV, Fig. 2a, Terborgh, 1985; Parker *et al.*, 1989; Ashton & Hall, 1992; Koike & Syahbuddin, 1993). In forests with more open upper canopies, including many needle-leaf forests, leaf area density can be predominantly accumulated in the lower canopy or understory layers (e.g., OSBS, PUUM, and WREF, Fig. 2a, Baldocchi *et al.*, 1997; Bonan, 2016; Hanberry *et al.*, 2020; Law *et al.*, 2001). Soil moisture conditions, topography, and gap formations following disturbances all alter foliage patterns (e.g., Bonan, 2016; Stark *et al.*, 2020; Almeida *et al.*, 2016; Hanberry *et al.*, 2020). In addition, seasonally dry and wet conditions, deciduousness, and phenology contribute to temporally shifting leaf area density patterns (Parker & Tibbs, 2004; Parker *et al.*, 2019). In this review, we focus on growing season conditions (peak leaf area index, LAI) unless otherwise noted.

Light, specifically the proportion of incident light and photosynthetically active radiation (PAR), decreases from the canopy top to the forest floor, with the profile shape modified by leaf area density, canopy height, and canopy structure across species and forest types (Fig. 2a-d, Supporting Information Figure S1, Koike *et al.*, 2001). This gradient is more pronounced in dense canopies, including broad-leaf and mixed forests (e.g., SCBI, SERC and HARV, Fig. 2d), than in open canopy forests, including many conifer forests (e.g., OSBS, PUUM, and WREF, Fig. 2d, Supporting Information Figure S1, Chazdon & Fetcher, 1984; Baldocchi *et al.*, 1997; Smith *et al.*, 2019; Aussenac, 2000; Bartemucci *et al.*, 2006; Tymen *et al.*, 2017; Parker *et al.*, 2019). Variability in the light environment decreases with height, with the shaded understory being highly influenced by sunflecks, or brief increases in solar radiation caused by small canopy gaps and wind-induced canopy movements (Way & Pearcy, 2012). Likewise, the mid-canopy experiences a highly variable light environment due to the sun's passage across a dynamically structured canopy surface (Way & Pearcy, 2012). The implication of this light gradient is that upper canopy leaves have higher potential photosynthetic rate (see section 4.2), but also greater propensity towards elevated T_{leaf} (see sections 2.2, 4.2).

Wind speeds are also higher at the top of the canopy, owing to the buffering effect of the canopy (Jucker *et al.*, 2018). This holds true across the range of forest types (Fig. 2e, Supporting Information Figure S1, Barnard & Bauerle, 2016; Hanberry *et al.*, 2018, 2020; Jucker *et al.*, 2018; McGregor *et al.*, 2021; Muller *et al.*, 2021) and savannas (Curtis *et al.*, 2019; Johnston *et al.*, 2020). Specifically, averaged across the NEON sites, maximum daily wind speeds were 4.1 m s^{-1} at the top of the vertical profile, compared to $\leq 1.1 \text{ m s}^{-1}$ at the bottom of the vertical profile. The implication is that upper canopy leaves have substantially higher boundary layer conductance (g_b) and therefore greater potential for both water and heat loss (see sections 2.2, 4.1).

Atmospheric concentrations of carbon dioxide (CO_2) and water vapor can also vary across the vertical gradient. Atmospheric CO_2 concentrations tend to be higher near the ground at night, associated with plant and soil respiration, although the elevated CO_2 quickly dissipates during the day (Yang *et al.*, 1999; Koike *et al.*, 2001). Elevated CO_2 may benefit understory seedlings operating close to their carbon compensation point, but given that

differences are negligible for most of the day when photosynthesis is occurring, gradients in CO₂ concentrations are unlikely to significantly affect the energy balance and metabolism of leaves across the forest vertical gradient.

Relative humidity (RH) tends to be higher in the understory and decreases with height, although this trend is absent in open forests (Fig. 2f, Supporting Information Figure S1, e.g., Jucker *et al.*, 2018; McGregor *et al.*, 2021). Dense-canopy forests maintain higher daily maximum RH in the understory than open forests and nearby open areas, an effect that is greater in wetter conditions, and warmer months (von Arx *et al.*, 2012; Hanberry *et al.*, 2020). In combination with T_{air} , RH determines vapor pressure deficit (VPD)– the driving force of water loss from leaves—which tends to be greater in the upper canopy and canopy gaps than in the understory (Niinemets & Valladares, 2004; Fauset *et al.*, 2018; Tymen *et al.*, 2017). Especially when canopy height and LAI are large, maximum T_{air} and VPD are reduced in the understory (Jucker *et al.*, 2018). The implication is that canopy leaves face higher g_b and associated potential for water and heat loss (see sections 2.2, 4.1).

Air temperature (T_{air}) often shows little variation across the vertical gradient, but under certain circumstances it can be significantly buffered by forest canopies (Fig. 2, Supporting Information Figure S1). The T_{air} gradient from the upper canopy to the understory varies with factors such as radiation fluxes, local topography, vertical air mixing, cloud cover and vegetation type (De Frenne *et al.*, 2021). Typically, dense canopies buffer understories from high maximum T_{air} more than open canopies, *i.e.*, dense canopy understories can have cooler maximum daytime T_{air} and warmer nighttime minimum T_{air} than open canopy understories or nearby clearings (Davis *et al.*, 2019a; De Frenne *et al.*, 2021, 2019; Rambo & North, 2009; von Arx *et al.*, 2012; Zellweger *et al.*, 2019; Misson *et al.*, 2007). Notably, this pattern can be reversed in open forests, where below-canopy maximum T_{air} can be warmer than canopy T_{air} due to turbulent air mixing and the thermal radiative flux from the soil and the canopy that is intercepted by lower-canopy layers, analogous to a ‘canopy greenhouse effect’ (e.g., OSBS, Fig. 2g, Supporting Information Figure S1b, Hadley & Smith, 1987; Rambo & North, 2009; Curtis *et al.*, 2019; Zweifel *et al.*, 2002; Hardwick *et al.*, 2015;

Banerjee *et al.*, 2017). These usually-modest gradients in T_{air} combine with the above-described gradients in micrometeorological conditions to shape T_{leaf} .

2. Leaf temperature

T_{leaf} is strongly tied to T_{air} , and is further influenced by other micrometeorological drivers (section 1) and by leaf traits and stomatal conductance (see sections 3-4), with leaves adjusting to their environment to approach, when possible, an optimal T_{leaf} for carbon assimilation and metabolic processes (Drake *et al.*, 2020; Perez & Feeley, 2020; Michaletz *et al.*, 2015). Leaves are typically cooler than the air at night, and under some daytime conditions (cloudy skies, high wind speeds, and high T_{air}). Leaves are typically warmer than air when under full sunlight, especially under slow wind speeds and low T_{air} (Doughty & Goulden, 2008). While T_{leaf} is rarely exactly equal to T_{air} , it is most commonly within a few degrees (Cavaleri, 2020).

2.1. Biophysical drivers of T_{leaf}

Fundamentally, T_{leaf} is determined by the energy balance of a leaf and can be estimated based on biophysical principles, where $T_{leaf} - T_{air}$ is a function of energy input from net radiation (R_n , including shortwave and longwave) minus heat lost to the environment (Fig. 3, Campbell & Norman, 1998; Muir, 2019). High R_n loads can elevate T_{leaf} dramatically above T_{air} (Fig. 3a). Sensible heat flux between leaf and air is regulated by leaf boundary layer conductance, which is greater in smaller leaves (Fig. 3d) and higher wind speeds (Fig. 3b). Latent heat flux (λE) through transpiration has a strong cooling effect, and is determined by stomatal and boundary layer conductances (g_s and g_b) and VPD, where g_b increases with wind speed and g_s can decline at high VPD due to stomatal closure. Therefore, $T_{leaf} - T_{air}$ decreases with wind speed (Fig. 3b, Daudet *et al.*, 1999), increases with RH (Fig. 3c), increases with leaf size (Fig. 3d), and decreases with g_s (Fig. 3e).

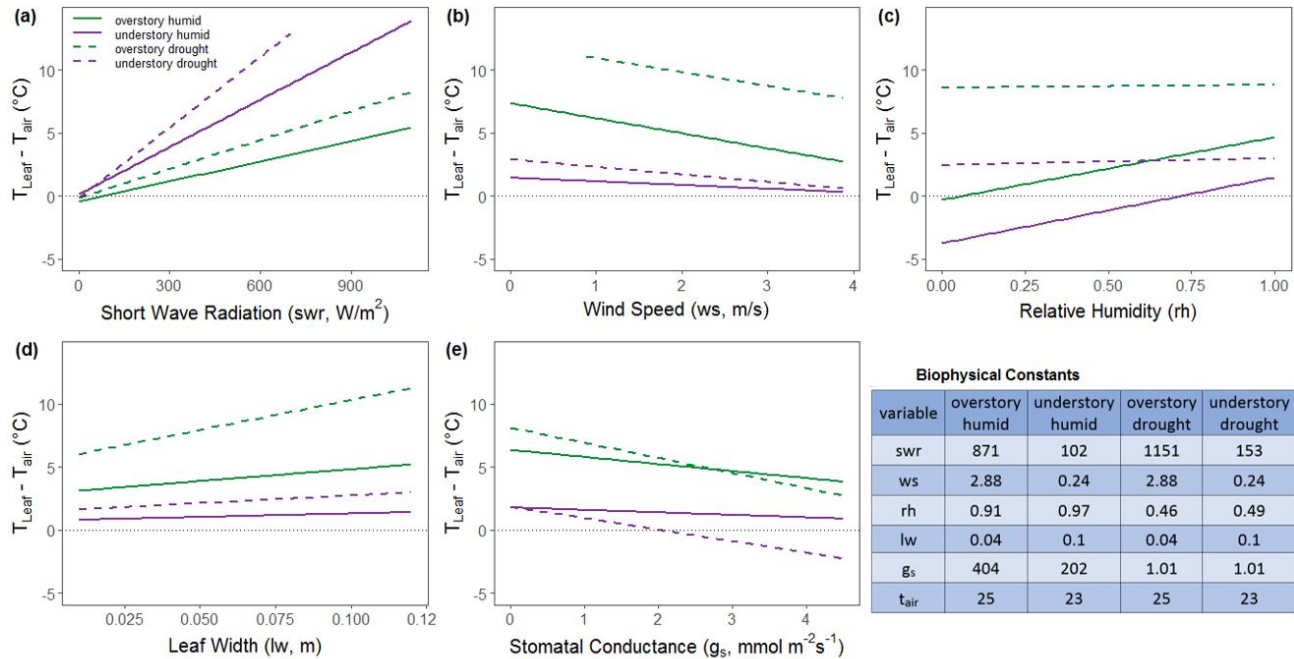


Figure 3. Theoretical expectations for variation in the difference between leaf and air temperatures, $T_{leaf} - T_{air}$, in response to (a) shortwave radiation, (b) wind speed, (c) relative humidity, (d) leaf width, and (e) stomatal conductance. Leaf temperatures were modeled using the *tealeaves* R package of Muir (2019) parameterized to represent a broadleaf species (*Quercus rubra* L.) in a mesic temperate forest (Harvard Forest, Massachusetts, USA) under both humid and drought conditions, as detailed in Supplementary Information Methods S2. In each scenario, the independent variable was allowed to vary while other parameters were held constant at the values given in the table of biophysical constants.

Under hot and dry conditions, leaves face a trade-off between T_{leaf} regulation and water conservation (Fauset *et al.*, 2018; Koch *et al.*, 1994). With adequate water, high λE can facilitate heat dissipation, particularly for leaves with smaller size (higher g_b) and larger g_s (Dong *et al.*, 2017; Leigh *et al.*, 2017; Song *et al.*, 2020; Konrad *et al.*, 2021; Leuzinger & Körner, 2007). However, when leaf water demand (influenced by VPD and stomatal opening) exceeds the rate of supply, conservation of water (g_s limitation) occurs at the cost of increasing T_{leaf} (Fig. 3e, Fauset *et al.*, 2018). Therefore, at high solar radiation loads, leaves can maintain T_{leaf} closer to T_{air} at maximum g_s , but during g_s limitation, solar

radiation can drastically elevate T_{leaf} above T_{air} , especially for larger leaves (Fauset *et al.*, 2018; Song *et al.*, 2020; Konrad *et al.*, 2021).

2.2 Vertical gradients in leaf temperature

The basic biophysical principles outlined above shape the tendency for T_{leaf} to be elevated above T_{air} across vertical gradients in closed-canopy forests. High radiation at the top of the vertical profile (Fig. 2) implies that canopy leaves have much greater tendency for high $T_{leaf} - T_{air}$, such that they would be expected to be warmer than understory leaves under most conditions (Fig. 3). However, higher wind speeds (Fig. 2) reduce $T_{leaf} - T_{air}$ (Fig. 3b, Niinemets & Valladares, 2004; Bonan, 2016). In addition, adaptive leaf traits that increase g_b and g_s (see sections 3, 4.1) mediate the direct effects of solar radiation on upper canopy leaves and result in higher rates of heat loss (Fig. 3b-e). In contrast, greater RH and lower wind speeds in the understory may limit λE (through reduced g_s and g_b), thereby increasing T_{leaf} (Fig. 3, Perez & Feeley, 2018; Tibbitts, 1979).

The propensity for T_{leaf} to be elevated above T_{air} is not expected to be uniform across time and space, but rather to vary with micrometeorological conditions. Under drought conditions (hot and dry, with higher-than-average solar radiation), when g_s is limiting, there will be a greater propensity for $T_{leaf} - T_{air}$ to be elevated in the canopy compared to the understory (Fig.3). This is because sun leaves are exposed to higher irradiance and VPD, and therefore have steeper g_s limitation than shade leaves (Fig. 3e, Leigh *et al.*, 2017; Fauset *et al.*, 2018). In contrast, under hot and wet conditions, higher wind speeds and g_b enable cooling in the upper canopy, whereas lower wind and g_b in the understory allow much less evaporative cooling (Fig. 3b,d, Roberts *et al.*, 1990a; Leigh *et al.*, 2017; Martin *et al.*, 1999; Song *et al.*, 2020). Thus, while understory and within-canopy shade leaves can remain cooler under lower radiation, their environment is not conducive to shedding excess heat, which in combination with their physiological propensities may result in above-optimal T_{leaf} under slight heat or drought stress, or when exposed to higher levels of radiation, for example during sunflecks (Leigh *et al.*, 2017; Song *et al.*, 2020; Schymanski *et al.*, 2013). In addition to lower wind speeds (Fig. 2), higher RH in the understory and inner

canopy (Fig. 2) would also inhibit cooling, as λE is stifled under high RH, resulting in greater $T_{leaf} - T_{air}$ (Fig. 3c, Tibbitts, 1979; Song *et al.*, 2020; Konrad *et al.*, 2021; Dietz *et al.*, 2007; Perez & Feeley, 2018).

Vertical T_{leaf} gradients are also expected to vary with canopy structure (Fig. 3). Forests with closed canopies and high LAI, including tropical and temperate broadleaf forests, act as a parasol, absorbing most of the incoming radiation and preventing vertical air mixing in the understory. Therefore, in these forests, leaves in the upper canopy can experience greater $T_{leaf} - T_{air}$ and higher maximum T_{leaf} than do buffered lower-canopies, in some cases exceeding the optima for photosynthesis (T_{opt}) because of g_s limitation and high solar radiation loads (Niinemets *et al.*, 1999; Doughty & Goulden, 2008; Fauset *et al.*, 2018; Pau *et al.*, 2018; Carter *et al.*, 2021; Rey-Sánchez *et al.*, 2016; Mau *et al.*, 2018; Miller *et al.*, 2021). In contrast, open canopies with lower LAI allow more vertical air mixing and sunlight into the understory. This mixing and light transmission can either neutralize a T_{leaf} gradient or elevate $T_{leaf} - T_{air}$ in the lower canopy relative to the upper canopy (Fig. 2h, Supporting Information Figure S1, Hadley & Smith, 1987; Martin *et al.*, 1999; Zweifel *et al.*, 2002; Muller *et al.*, 2021). The latter can result from a combination of still air in the lower canopy, and the ‘canopy greenhouse effect’ or sunflecks, as mentioned above (Schymanski *et al.*, 2013; Hardwick *et al.*, 2015), and because shade leaves tend to have lower g_s and greater thermal capacitance (capacity to hold heat, Schymanski *et al.*, 2013). Similarly, in very open forests or savannas, trees growing close to the ground can experience greater heat stress in their lower than upper canopies (Hadley & Smith, 1987; Curtis *et al.*, 2019; Johnston *et al.*, 2020). One of the few remote sensing studies combining drone lidar and thermal data found strong vertical gradients in midday plant temperature with $\sim 5^\circ\text{C}$ cooler temperatures lower in the canopy of a dense forest stand in the sub-alpine Eastern Swiss Alps (Webster *et al.*, 2018). However, the opposite trend was observed for a lone tree surrounded by grass in the same area, with cooler temperatures at the top of the tree crown, indicating a strong influence of closed-canopy shading on vertical temperature gradients.

295 **3. Leaf traits**

296 Leaf traits shape T_{leaf} , leaf metabolism, and leaf thermal sensitivity across forest vertical
297 strata (Zwieniecki *et al.*, 2004; Michaletz *et al.*, 2015, 2016). Leaf morphology adjusts to the
298 previously experienced microenvironment during leaf formation in buds, and also during
299 ongoing leaf expansion (Zwieniecki *et al.*, 2004), and the ratio of far red to red light and
300 associated water demands determine the differentiation of traits of sun and shade leaves
301 (Zwieniecki *et al.*, 2004; Casas *et al.*, 2011; Keenan & Niinemets, 2016). This dichotomy in
302 leaves is observed along the vertical gradient where canopy-leaves vary dramatically from
303 canopy-interior and understory due to the differences in biophysical conditions (Fig. 2).

304 Across the vertical gradient, traits vary (1) across sun and shade leaves within individuals,
305 (2) across canopy and understory individuals of the same species, and (3) across canopy
306 and understory species. The majority of studies characterizing variation in leaf traits or
307 metabolism examine intraspecific patterns (categories 1 and 2), which are therefore the
308 main focus of this review (Table 1). However, when it comes to understanding and
309 modeling forest ecosystem function, given that species traits strongly shape the propensity
310 for trees to inhabit understory vs. canopy positions, ecosystem function is also shaped by
311 interspecific trait variation (e.g., Cavaleri *et al.*, 2010).

312 **3.1. Intraspecific trait variation**

313 Within-canopy, leaf traits vary along the vertical light gradient (*i.e.*, sun and shade leaves,
314 Casas *et al.*, 2011) at a biochemical, anatomical and structural level (Table 1, Sack *et al.*,
315 2006; Niinemets *et al.*, 2015a; Chen *et al.*, 2020). Much of our understanding of trait
316 coordination is based on the leaf economics spectrum concept developed across diverse
317 species (Wright *et al.*, 2004), which was developed using sun leaves (Chen *et al.*, 2020;
318 Keenan & Niinemets, 2016), so further research is needed to characterize trait
319 relationships and responses vertically through the full range of canopy microenvironments.
320 It has been established that independently of the light environment, traits also vary within
321 species along the ontogenetic trajectory from the understory to the canopy. For example,
322 leaf mass per area (LMA), photosynthetic capacity (A_A) and g_s have been observed to

323 increase with height, independently of light (Cavender-Bares & Bazzaz, 2000; Thomas &
324 Winner, 2002; Houter & Pons, 2012). Therefore, ontogeny is bound to play a role in shaping
325 leaf traits and thermal sensitivity (Carter *et al.*, 2021; Niinemets, 2010a).

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Table 1. Summary of observed variation in Leaf gas exchange and its thermal sensitivity across the vertical gradient and/or between sun and shade leaves. Studies listed here were compiled using a systematic review process, as described in Supplementary Information Methods S3.

trait	symbol	units	response*	forest type(s) [†]	reference(s) [‡]
Leaf anatomy and morphological traits					
leaf area	LA	cm ²	↓ H	TrB, TeB, BoN	7, 8, 10
			↓ L	TrB, TeB, BoN	7, 8, 3, 10
leaf mass per area (or inverse of specific leaf area)	LMA (or 1/SLA)	g cm ⁻²	↑ H	TrB, TeB, TeN, BoN	1, 7, 2, 3, 4, 6
leaf thickness		μm	↑ L	TrB, TeB, TeN, BoN	1, 7, 2, 3, 5, 6
			↑ H	TrB, TeB, TeN	15, 11, 2, 13, 16
leaf density		g cm ⁻³	↑ L	TrB, TeB, TeN	11, 15, 2, 5
			↑ H	TeB	2
			↑ L	TrB, TeB	6, 2
			≈ L	TeN	5
pinnate lobation		cm ²	↑ H	TeB	3
			↓ H	TeB	8
			↑ L	TeB	8, 3
leaf packing		n /cm stem	↑ L	TeN	25, 26
blade inclination angle (vertical)	φB	°	↑ H	TrB, TeB	21, 22, 23
			↑ L	TrB, TeB	21, 24, 23, 22, 48
trichome density		mm ⁻²	↑ H	TrB	17
			↑ L	TrB, TeB	17, 18, 19, 20
stomatal density	D _{stomata}	mm ⁻²	↑ H	TrB, TeB, TeN	11, 12, 3, 13, 4
			↑ L	TrB, TeB	12, 11, 3
total vein density	VLA	mm mm ⁻²	↑ H	TeB	46
			↑ L	TeB	46, 47
minor vein density	VLA _{min}	mm mm ⁻²	↑ H	TeB	14
			↑ L	TeB	14, 47
upper cuticle thickness	CT	μm	↑ H	TrB, TeN	27, 4
			↑ L	TrB, TeB	27, 28
Traits related to metabolic capacity and efficiency					
nitrogen content	N	g m ⁻²	↑ H	TrB, TeB, TeN, BoN	7, 29, 30, 32, 31, 9
		mg g ⁻¹	≈↓ H	TrB, TeB, TeN	15, 7, 29, 30, 32, 34
			≈↓ L	TrB, TeB, TeN	7, 35, 29, 30, 32, 5
phosphorous content	P	g m ⁻²	↑ H	TrB, TeB, TeN	15, 36, 1, 37
			↑ L	TrB, TeB, TeN	15, 5
			≈ L	TrB, TeB	1
		mg g ⁻¹	≈↓ H	TrB	15, 35, 1
			≈ L	TrB, TeB	15, 35, 1
chlorophyll content	Chl	mg	↓ H	TrB, TeB	40, 41

333 Table 1, cont.

trait	symbol	units	response*	forest type(s) [†]	reference(s) [‡]
		cm ⁻²			
chlorophyll a/b ratio	<i>chl a/b</i>	mol mol ⁻¹	↓ L	TrB, TeB	42, 41
			↑ H	TrB, TeB, BoN	42, 30, 6
			↑ L	TrB, TeB, BoN	42, 30, 39, 22, 6
carbon isotope composition	$\delta^{13}C$	‰	↑ H	TrB, TeB, TeN	7, 43, 31
			↑ L	TrB, TeB, TeN	7, 29, 31
Intercellular CO ₂ concentration	<i>C_i</i>	μmol mol ⁻¹	↓ H	TeB	30, 44
			↓ L	TeB	30, 44
Light absorption or reflectance					
PAR absorptance		% nm	≈ H	TrB	42, 45
			≈↑ L	TrB	42, 45
absorptance efficiency per unit biomass		% g ⁻¹	↓ H	TrB	42, 45
PAR transmittance		%	↓ L	TrB	42, 45
			↓ H	TrB	42, 45
Reflectance		%	↓ L	TrB	42, 45
			≈ H	TrB	42, 45
			↑ H	BoN	6
			≈ L	TrB	42, 45
Biochemical protection against light and heat damage					
β-carotene and lutein		μmol m ⁻²	↑ H	TrB, TeB, BoN	30, 42, 6
			↑ L	TrB, TeB, BoN	30, 38, 6
xanthophyll cycle pigments	<i>VAZ</i>	μmol m ⁻²	↑ H	TrB, TeB	38, 30, 22
			↑ L	TrB, TeB	39, 30
isoprene emission ability	<i>I</i>	nmol m-2 s-1	↑ H	TrB	49
			(peak in mid-canopy)		
			↑ L	TrB	49
			(peak in mid-canopy)		
			↑ L	TeB	50

334

335 *Responses across height and light gradients are summarized, with up and down arrows indicating
 336 significant increasing or decreasing trends, respectively, in response to height (H) or light (L). ≈
 337 indicates lack of any notable directional variation, and ≈ ↑ or ≈ ↓ indicate non-significant or mixed
 338 trends (e.g., significant in some but not all species studied).

339 † Forest types are coded as follows: TrB = tropical broadleaf; TeB = temperate broadleaf; TeN =
 340 temperate needleleaf (conifer); BoN= boreal needleleaf (conifer).

‡ 1. Mau et al. 2018; 2. Coble and Cavaleri 2014; 3. Sack et al. 2006; 4. Chin and Sillett 2019; 5. Wyka et al. 2012; 6. Atherton et al. 2017; 7. Kenzo et al. 2015; 8. Kusi and Karasi 2020; 9. Dang et al. 1997; 10. Gebauer et al. 2015; 11. Marengo et al. 2017; 12. Kafuti et al. 2020; 13. Van Wittenberghe et al. 2012; 14. Zhang et al. 2019; 15. Weerasinghe et al. 2014; 16. Oldham et al. 2010; 17. Ichie et al. 2016; 18. Gregoriou et al. 2007; 19. Levizou et al. 2005; 20. Liakoura 1997; 21. Fauset et al. 2018; 22. Niinemets et al. 1998; 23. Ishida et al. 1998; 24. Millen and Clendon 1979; 25. Smith and Carter, 1988; 26. Hadley and Smith 1987; 28. Baltzer and Thomas 2005; 29. Coble et al. 2016; 30. Scartazza et al. 2016; 31. Duursma and Marshall, 2006; 32. Harley et al. 1996; 33. Hernandez et al. 2020; 34. Turnbull et al. 2003; 35. Chen et al. 2020; 36. van de Weg et al. 2012; 37. M.A Cavaleri et al. 2008; 38. Koniger et al. 1995; 39. Mastubara et al. 2009; 40. Harris and Medina 2013; 41. Hansen et al. 2001; 42. Poorter et al. 1995; 43. Coble et al. 2016; 44. Niinemets et al. 2004; 45. Poorter et al. 2000; 46. Zwieniecki et al. 2004; 47. Sack and Scoffoni, 2013; 48. Ball et al., 1988; 49. Taylor et al. 2021; 50. Niinemets et al. 2010

Sun leaves have anatomical, morphological, and physiological traits that reduce heat due to higher conductance (g_b or maximal g_s) and/or reflectance, which help to lower $T_{leaf}-T_{air}$ (Table 1). Thus, sun leaves are generally smaller, thicker, with higher leaf mass per area, and are more deeply lobed (Fig. 3, Vogel, 1968; Zwieniecki *et al.*, 2004; Sack *et al.*, 2006; Leigh *et al.*, 2017; Mathur *et al.*, 2018), but with greater leaf packing and clumping (reduces g_b). Steeper leaf angles reduce radiation loads and thereby decrease $T_{leaf} - T_{air}$ (Ball *et al.*, 1988; Niinemets, 1998), while higher trichome density increases reflectance, thereby also decreasing radiation load. Further, sun leaves tend to have higher stomatal and vein densities, which enable higher maximal g_s and thereby facilitate effective cooling (see section 4.1, Zwieniecki *et al.*, 2004). At the same time, sun leaves also have adaptations to protect against water stress, particularly in drier climates, including greater cuticle thickness and higher trichome density (reduces g_b or increases boundary layer turbulence, Schreuder *et al.*, 2001; Ichie *et al.*, 2016). In contrast, shade leaves have traits that maximize light capture in the diffuse-light environment with sunflecks (e.g., lower LMA and higher light absorptance efficiency per unit biomass), but larger leaf size and lower transpiration makes them more prone to overheating than sun leaves (Casas *et al.*, 2011; Leigh *et al.*, 2017; Schymanski *et al.*, 2013). In open canopies, where light is comparatively

homogeneous, leaf traits may be more shaped by maximum T_{air} and VPD stress than by light (Mediavilla *et al.*, 2019).

Most leaf biochemical traits also vary across light and height gradients (Table 1), both shaping and resulting from gradients in metabolism (see section 4, Table 2). Sun leaves have higher concentrations (per unit area) of elements such as nitrogen (N_{area}) and phosphorus (P_{area}) that are critical to leaf metabolism, including respiration (Meir *et al.*, 2001; Weerasinghe *et al.*, 2014) and photosynthetic processes (Niinemets & Valladares, 2004; Weerasinghe *et al.*, 2014; Scartazza *et al.*, 2016). Increases in chlorophyll a/b ratios with height reflect the greater light availability in the upper canopy, while greater chlorophyll concentrations at lower heights within the canopy give shade leaves greater PAR absorptance efficiency (Table 1). Higher photosynthetic rates (per unit leaf area) and more frequent stomatal closure higher (see section 4, Table 2) result in lower intercellular CO_2 concentrations and higher $\delta^{13}C$ concentrations in leaf tissues (Table 1).

Biochemical protection against foliage light and heat damage also increases with irradiance, and thus tends to be higher in the upper canopy than in the understory (Table 1). Carotenoids (e.g., beta carotene and lutein), including xanthophyll cycle pigments (i.e., violaxanthin, antheraxanthin and zeaxanthin, VAZ), can play a role in antioxidant scavenging and converting excess excitation energy into heat to reduce photoinhibition (Niinemets *et al.*, 1998; Niinemets, 2007; Mathur *et al.*, 2018). The dissipation of excess light energy is also important for leaf acclimation to higher temperatures if high T_{leaf} impairs the photochemical energy dissipation pathway (Havaux & Tardy, 1996). Capacity for heat-sensitive, light-dependent (photosynthetically linked) emissions of volatile organic compounds (VOCs), including isoprene and monoterpenes, enhances photosynthetic thermal tolerance by regulating antioxidant defenses and other metabolic processes (Copolovici *et al.*, 2005; Vickers *et al.*, 2009; Taylor *et al.*, 2019; Sharkey *et al.*, 2008; Riedlmeier *et al.*, 2017; Monson *et al.*, 2021). Less than half of tree species express significant light-dependent emissions (Taylor *et al.*, 2018; Kesselmeier & Staudt), such that variation in emissions across the vertical profile can be influenced both by vertical

variation in species compositions and plasticity in emission rate capacities (see section 4.4, Taylor *et al.*, 2021).

The vertical structure of microenvironments likely influences forest photosynthetic capacity (Rey-Sánchez *et al.*, 2016) via leaf phenology. In deciduous forests, the timing and extent of seasonal leaf gain and loss is structured across the vertical profile. For example, in a temperate deciduous forest, spring bud-break tended to occur earlier among juvenile trees in the more sheltered understory, where temperature sums accumulated more rapidly, than among conspecific canopy trees (Augspurger & Bartlett, 2003). Within tropical dry-deciduous species in Panama, the fraction of seasonally deciduous individuals increased toward larger tree size classes in hotter, brighter environments, with understory individuals typically remaining evergreen (Condit *et al.*, 2000). Even in evergreen forests, environmental variation alters leaf age distributions (Albert *et al.*, 2019), which affects forest photosynthetic capacity (Wu *et al.*, 2016; Niinemets, 2016) and heat stress via age-specific leaf function (Albert *et al.*, 2019). For instance, in tropical evergreen forests, because leaf turnover rates of sun leaves in the upper canopy is faster than in the subcanopy, less damage accumulates (Miller *et al.*, 2021). Leaf age affects vulnerability to heat stress and has a strong effect on metabolism (Marias *et al.*, 2017; Kikuzawa & Lechowicz, 2006; Zhou *et al.*, 2015), and can be expected to similarly scale through vertically structured phenology to affect forest responses to heat anomalies.

3.2. Interspecific trait variation

Vertical gradients in the biophysical environment shape which plant strategies, or sets of traits, are competitive in canopy versus understory conditions, thereby shaping community composition across size classes. Generally, the pattern of fundamental trait adaptations to light gradients across forest species is similar to within-species trends in traits and sometimes metabolism (Thomas & Winner, 2002; Rozendaal *et al.*, 2006; Houter & Pons, 2012). For instance, across increasing tree size classes, there is an increase in the fractions of species that are deciduous (mirroring the fraction of individuals, Condit *et al.*, 2000; Meakem *et al.*, 2018). However, exceptions exist: at least among evergreen species, shade tolerant species tend to have higher LMA than light demanding species, by contrast with

the generally higher LMA for sun than shade leaves within canopies (Lusk *et al.*, 2008). Further, the range in trait values can be several times greater in multi-species canopy than in understory species, based on their inherent species-specific traits and responses to environmental conditions. Therefore, vertical gradients in T_{leaf} and metabolism within forest ecosystems are underpinned by both intra- and inter-specific variation in traits.

4. Leaf gas exchange and its thermal sensitivity

Leaf metabolism is strongly shaped by T_{leaf} , and by the traits and environmental drivers reviewed above, all of which vary across vertical forest gradients (Fig. 1). However, as we detail below, few studies have evaluated temperature responses of leaf metabolic rates along a vertical canopy gradient, or compared sun and shade leaves (Table 2).

Table 2. Summary of observed variation in Leaf gas exchange and its thermal sensitivity across the vertical gradient and/or between sun and shade leaves. Studies listed here were compiled using a systematic review process, as described in Supplementary Information Methods S3.

trait	symbol	units	response*	forest type(s) [†]	reference(s) [‡]
Conductance					
boundary-layer conductance	g_b	$\text{mmol m}^{-2} \text{s}^{-1}$	↑ H	TrB	3
		mm s^{-1}	↑ H	TeN	12
			≈ L	TeN	12
leaf hydraulic conductance	K_{leaf}	$\text{m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$	↑ L	TeB	41
cuticle conductance	g_{min}	$\text{mmol m}^{-2} \text{s}^{-1}$	↑ L	TrB	47
max stomatal conductance	$g_{s \max}$	$\text{mol m}^{-2} \text{s}^{-1}$	↑ H	TrB, TeB, BoN	1, 2, 4
			↑ L	TrB, TeB, TeN, BoN	8, 9, 10, 7, 4
stomatal conductance limitation	g_s	$\text{mol m}^{-2} \text{s}^{-1}$	↑ H	TrB, TeN	9, 40, 5, 6, 7
stomatal conductance at optimal temperature	$g_s \text{ at } T_{opt}$	$\text{mol m}^{-2} \text{s}^{-1}$	↑ L	TrB, TeN	9, 40, 7
			≈↑ H	TeB	11
			↓ H	TrB	40
			≈↑ L	TrB	8
Photosynthesis					
maximum photosynthetic capacity	A_{max}	$\text{mol m}^{-2} \text{s}^{-1}$	↑ H	TrB, TeB, BoN	14, 11, 15, 4
			≈↓ H	TeB	16
			↑ L	TrB, TeB, TeN, BoN	14, 17, 18, 19, 10, 4
			≈ H	TrB	20, 21
			≈ L	TrB, TeB, TeN	20, 21, 19
maximum light-saturated net photosynthesis	A_{sat}	$\mu\text{mol m}^{-2} \text{s}^{-1}$	↑ H	TrB, TeB	22, 23
A_{sat} at optimum temperature	A_{opt}	$\mu\text{mol m}^{-2} \text{s}^{-1}$	↑ L	TrB, TeB	8, 23
			≈↑ H	TrB, TeB	13, 11
			↑ H	TrB	40
			↑ L	TrB	8, 13

445 Table 2, cont.

trait	symbol	units	response*	forest type(s) [†]	reference(s) [‡]
optimum temperature for photosynthesis	T_{opt}	°C	≈ H	TrB, TeB	24, 11, 13
			↓ H	TrB	40
			≈ L	TrB, TeB	9, 8, 11
photosynthetic light compensation point	LCP	μmol m ⁻²	↑ H	TrB, TeB, TeN	25, 16
			↑ L	TrB, TeB, TeN	8, 17, 16
maximal carboxylation rate	V_{cmax}	μmol m ⁻² s ⁻¹	↑ H	TrB, TeB	2, 23, 14
		nmol g ⁻¹ s ⁻¹	↑ L	TrB, TeB, BoN	9, 23, 14, 10
			≈ H	TrB, TeB	2, 23
			≈ L	TrB, TeB	2, 23
		nmol CO ₂ g ⁻¹ s ⁻¹	≈ ↓ L	TeB	26
optimum temperature for V_{cmax}	$V_{cmax}(T_{opt})$	μmol m ⁻² s ⁻¹	≈ ↑ H	TeB	11
			≈ L	TrB	9
electron transport rate	J_{max}	μmol m ⁻² s ⁻¹	↑ H	TrB, TeB	2, 40, 23, 14
			↑ L	TrB, TeB	9, 23, 27, 14
		nmol g ⁻¹ s ⁻¹	≈ H	TrB, TeB	2, 23
			≈ L	TrB, TeB	2, 23
		nmol e ⁻¹ g ⁻¹ s ⁻¹	≈ ↓ L	TeB	26
optimal temperature of J_{max}	T_{optETR}	°C	↓ H	TrB	40
	$J_{max}(T_{opt})$	μmol m ⁻² s ⁻¹	≈ L	TrB	9
high-temperature CO ₂ compensation point	T_{max}	°C	≈ H	TrB	22
			≈ L	TrB	8
photosynthetic heat tolerance	T_{50}	°C	↓ H**	TrS	31
			≈ ↑ L	TrB, TeB	8, 17
critical temperature beyond which Fv/Fm declines	T_{crit}	°C	≈ ↑ L	TrB, TeB	8

446

447

448 Table 2, cont.

trait	symbol	units	response*	forest type(s) [†]	reference(s) [‡]
Respiration					
respiration rate at 25 °C	<i>R</i>	μmol CO ₂ m ⁻² s ⁻¹	↑ H	TrB, TeB, TeN	40, 32, 33, 34
		μmol CO ₂ kg ⁻¹ s ⁻¹	≈ H	TrB, TeB, TeN	32, 33
light respiration	<i>R_L</i>	μmol m ⁻² s ⁻¹	↑ L	TrB, TeN	32, 34,
			↑ H	TrB	22
dark respiration	<i>R_{dark}</i>	μmol m ⁻² s ⁻¹	↑ L	TrB	22
			↑ H	TrB, TeB, BoN	22, 14, 35, 23, 39
<i>R_{dark}</i> at reference <i>T</i>	<i>R_{dark}</i> at reference <i>T</i>	μmol m ⁻² s ⁻¹	↑ L	TrB, TeB, TeN, BoN	22, 14, 23, 17, 10, 39
			≈↑ H	TrB	2, 36
			≈ L	TrB	2, 36
			↑ H	TrB, TeB, TeN	22, 14, 35, 33
temperature sensitivity of <i>R_{dark}</i>	<i>Q₁₀</i>	μmol (kg leaf) ⁻¹ s ⁻¹	↑ H	TrB, TeB, TeN	22, 14, 35, 33
		μmol (kg N) ⁻¹ s ⁻¹	↑ H	TeB,TeN	35, 33
		μmol m ⁻² s ⁻¹	↑ L	TrB, TeB	22, 8, 35.
		°C ⁻¹	≈ H	TrB, TeB, TeN	22, 40, 35, 34
		°C ⁻¹	≈ ↑ H	TeB, TeN	37, 33
activation energy of <i>R_{dark}</i>	<i>E₀</i>	kJ mol ⁻¹ K ⁻¹	≈ ↓ L	TrB, TeB, TeN	22, 35, 34
			↑ L	TeB	37
			≈ H	TrB, TeB, TeN	22, 38, 33
VOC production					
isoprene emission (in emitting species)	<i>I</i>	nmol m ⁻² s ⁻¹	≈ L	TrB	22, 8
			↑ H (peak in mid-canopy)	TrB	42
			↑ L (peak in mid-canopy)	TrB	42
monoterpenoid emissions	<i>MT</i>	μg m ⁻² s ⁻¹	↑ H (peak in mid-canopy)	TeB	37, 43
			↑ L (peak in mid-canopy)	TeB	37, 44, 45
			↑ H (peak in mid-canopy)	TeB	46
			↑ L (peak in mid-canopy)	TeB	46

449

*Responses across height and light gradients are summarized, with up and down arrows indicating significant increasing or decreasing trends, respectively, in response to height (H) or light (L). \approx indicates lack of any notable directional variation, and $\approx \uparrow$ or $\approx \downarrow$ indicate non-significant or mixed trends (e.g., significant in some but not all species studied).

† Forest types are coded as follows: TrB = tropical broadleaf; TeB = temperate broadleaf; TeN = temperate needleleaf (conifer); BoN= boreal needleleaf (conifer).

‡ 1. Kafuti et al. 2020; 2. Van Wittenberghe et al. 2012; 3. Roberts et al. 1990; 4. Dang et al. 1997; 5. Marengo et al. 2017; 6. Ambrose et al. 2015; 7. Zweifel et al. 2001; 8. Slot et al. 2019; 9. Hernandez et al. 2020; 10. Urban et al. 2007; 11. Carter and Cavaleri 2018; 12. Martin et al. 1999; 13. Mau et al. 2018; 14. Kosugi et al. 2012; 15. Niinemets et al. 2015; 16. Bachofen et al. 2020; 17. Hamerlynck and Knapp 1994; 18. Coble et al. 2017; 19. Wyka et al. 2012; 20. Rijkerse et al. 2000; 21. Ishida et al. 1999; 22. Weerasinghe et al. 2014; 23. Scartazza et al. 2016; 24. Miller et al. 2021; 25. Harris and Medina 2013; 26. Legner et al. 2014; 27. Kitao et al. 2012; 28. Fauset et al. 2018; 29. Rey-Sanchez et al. 2016; 30. Muller et al. 2021; 31. Curtis et al. 2019; 32. Mier et al. 2001; 33. Turnbull et al. 2003; 34. Araki et al. 2017; 35. Bolstad et al. 1999; 36. Kenzo et al. 2015; 37. Harley et al. 1996; 38. Xu and Griffin 2006; 39. Atherton et al. 2017; 40. Carter et al. 2021; 41. Sack et al. 2003; 42. Taylor et al. 2021; 43. Harley et al. 1997; 44. Niinemets and Sun, 2014; 45. Sharkey and Monson, 2014; 46. Simpraga et al. 2013

** composite climatic stress variable from canopy temperature, vapour pressure deficit, and relative humidity is higher in lower canopy

4.1. Conductance

Leaf hydraulic, stomatal, and g_b are all critical for latent heat loss, which in turn can be important for regulating T_{leaf} (Fig. 3). Due to higher wind, lower RH, and smaller leaf sizes in the canopy (Fig. 2, Table 1), g_b increases with height (Table 2). Maximum g_s increases with light, and is thus higher in the sun-exposed upper canopy than in sub-canopy or understory leaves (Table 2). However, because water supply often cannot meet the demands incurred by the high irradiance and g_b experienced by sun leaves, midday stomatal depression is more prevalent in sun leaves than shade leaves in closed-canopy forests (Table 2), which drives the lower intracellular CO₂ and carbon isotope discrimination discussed in section 3.1 (Table 1). In sun leaves, T_{leaf} thus further increases

due to the lack of transpirational cooling (Zwieniecki *et al.*, 2004; Koch *et al.*, 1994; Kosugi & Matsuo, 2006; Sanches *et al.*, 2010). The temperature at which g_s is maximized, T_{opt} of g_s , did not differ significantly between sun and shade leaves in three tropical tree species (Slot *et al.*, 2019), but sun leaves in the upper canopy show a stronger decrease in g_s in response to rising T_{air} than do shade leaves in the lower canopy (Carter *et al.*, 2021; Hernández *et al.*, 2020). This, added to the tendency for sun leaves to have higher T_{leaf} , implies that high T_{air} should decrease g_s of canopy leaves more than understory leaves, particularly when water availability is limited.

4.2. Photosynthesis

Photosynthetic capacity is generally higher in exposed canopy positions– a fact that is both theoretically expected and observed in numerous field studies (Table 2, Niinemets, 2007 ; Chen *et al.*, 2020; Slot *et al.*, 2019; Kenzo *et al.*, 2015). This is primarily driven by the greater light available to sun leaves, which also have traits enabling higher photosynthetic rates under conditions of high light and sufficient water (Tables 1, 2).

Temperature can affect photosynthesis via direct and indirect pathways: directly, by altering photosynthetic enzyme activity and the electron transport chain, and indirectly through increased VPD causing stomatal closure (Lloyd & Farquhar, 2008). Photosynthesis has a peaked response to T_{air} , with the peak commonly corresponding to the prevalent ambient growing season temperature (Doughty & Goulden, 2008; Slot & Winter, 2017; Tan *et al.*, 2017). Beyond the optimum, photosynthesis decreases as a result of stomatal closure (e.g. Slot & Winter, 2017; Grossiord *et al.*, 2020; Smith *et al.*, 2020; Fredeen & Sage, 1999), and eventually due to biochemical constraints (Sharkey, 2005; Sage & Kubien, 2007; Vårhammar *et al.*, 2015; Kumarathunge *et al.*, 2019).

We have very little evidence as to how the temperature sensitivity of photosynthesis compares between sun and shade leaves, and existing studies reveal no pronounced overall trend with height in the optimum temperatures for photosynthetic processes (Table 2). Based on consistent positive relationships between growth temperature and optimum temperature of photosynthesis (T_{opt}) across sites and seasons (e.g. Tan *et al.*, 2017;

Kumarathunge *et al.*, 2019), one might expect sun leaves to have a stronger temperature-dependence and higher temperature optima than shade leaves (Campbell & Norman, 1998; Niinemets *et al.*, 1999; Niinemets & Valladares, 2004). However, such a trend is not apparent among recent studies, where for three species in Panama, the T_{opt} for sun leaves tended to be moderately, but not significantly, higher than that of shade leaves (Slot *et al.*, 2019; Hernández *et al.*, 2020). Similarly, T_{opt} of RuBP carboxylation ($V_{c_{max}}$) and regeneration rates (J_{max}) did not differ systematically between tropical sun and shade leaves (Hernández *et al.*, 2020), and along vertical gradients of tropical and temperate trees (Mau *et al.*, 2018; Miller *et al.*, 2021). In contrast, tropical experimental warming observations showed that T_{opt} and T_{opt} of J_{max} decrease from the understory to the canopy, potentially linked to greater thermal sensitivity of g_s in upper canopy leaves (Carter *et al.*, 2021). Hernández *et al.* (2020) also speculated that the observed lack of sun-shade differences in T_{opt} may reflect acclimation to similar temperatures of peak photosynthesis. Sun leaves experience higher temperatures, but maximum temperatures are associated with conditions of midday stomatal depression, and acclimation to optimize photosynthesis at these temperatures would not be advantageous. Shade leaves that do not experience midday depression continue to fix carbon even when afternoon air temperatures peak (Miller *et al.*, 2021). Evaluating this would require diurnal monitoring of net photosynthesis across a vertical profile through the canopy. In the meantime, it remains unresolved whether photosynthesis is more affected by high temperatures in canopy or understory leaves, and how this might vary across forest types and environmental conditions.

At very high T_{leaf} (~40-60 °C), photosystem II incurs irreversible damage, eventually leading to leaf necrosis and death (Baker, 2008; Feeley *et al.*, 2020; Kunert *et al.*, in press). Thermal tolerance is described in terms of the temperature at which efficiency of photosystem II starts to decrease, T_{crit} , and the T_{leaf} at which efficiency of photosystem II had decreased by 50%, T_{50} (Slot *et al.*, 2021a). Thermal tolerances vary across species, with more variation explained by leaf traits than phylogeny (Feeley *et al.*, 2020; Slot *et al.*, 2021a); for example, among tropical species, T_{crit} and T_{50} were found to be high in species

with large leaves with high thermal capacitance and those with high LMA, respectively (Slot *et al.*, 2021a). Thermal tolerances vary globally across latitude and climate, where T_{50} and T_{crit} decrease across increasing latitudes, and with elevation among tropical forests (O'Sullivan *et al.*, 2017; Feeley *et al.*, 2020; Slot *et al.*, 2021a). However, they are more closely adapted to microclimate than macroclimate (Feeley *et al.*, 2020; Slot *et al.*, 2021a). For example, *Quercus muehlenbergii* growing in xeric, sunnier conditions showed higher T_{50} by 2 °C than *Quercus macrocarpa* growing in shaded mesic conditions (Hamerlynck & Knapp, 1996). In Australia, along a vertical gradient within the canopy, *Acacia papyrocarpa* showed greater T_{50} and higher composite climate stress in the lower, north-facing canopy than other canopy positions, correlating with low wind speed, greater radiation and T_{air} , and lower rates of heat dissipation, as indicated by longer leaf thermal time constants (Curtis *et al.*, 2019). Across species sun leaves that experienced higher maximum temperatures show higher photosynthetic heat tolerance (Perez & Feeley, 2020). However, considering sun and shade leaf differences within canopy (Table 1), T_{50} varies modestly, being slightly lower for shade than sun leaves for two of three tree species in Panama (Slot *et al.*, 2019). The small difference in T_{50} coupled with larger differences in T_{leaf} across thermal microenvironments implies that more thermally tolerant leaves tend to operate closer to their thermal limits and could therefore be more vulnerable to heat anomalies (Perez & Feeley, 2020).

4.3. Respiration

Similar to photosynthesis, respiration tends to be higher in canopy sun-leaves (Table 2, Chen *et al.*, 2020), but its temperature sensitivity (Q_{10} or E_0 , Table 2) shows no definite trend along the vertical gradient (Bolstad *et al.*, 1999; Weerasinghe *et al.*, 2014). Specifically, the temperature sensitivity of respiration can be constant within vertical profiles and in seedling sun vs. shade leaves (Xu & Griffin, 2006; Zaragoza-Castells *et al.*, 2008, 2007; Carter *et al.*, 2021; Bolstad *et al.*, 1999; Weerasinghe *et al.*, 2014), greater in upper-canopy leaves (Turnbull *et al.*, 2003; Harley *et al.*, 1996), or greater in the lower canopy (Griffin *et al.*, 2002). This variation may be attributable to forest type, leaf traits and age (e.g., greater Q_{10} in younger leaves, Zhou *et al.*, 2015), or acclimation to high

temperature that decreases Q_{10} (Carter *et al.*, 2021; Slot & Kitajima, 2015). Overall, however, we currently lack synthetic understanding of how and why the temperature sensitivity of respiration varies across the forest vertical profile.

4.4. VOC emissions

Emission of the VOCs isoprene and a diversity of monoterpenes are similarly light and temperature sensitive, and play similar roles in photosynthetic thermal tolerance (Copolovici *et al.*, 2005; Vickers *et al.*, 2009; Taylor *et al.*, 2019; Sharkey *et al.*, 2008). In contrast to VOCs stored in oils that are released passively by heat and wounding, such as the monoterpenes responsible for pine scent, light-dependent emissions are linked to photosynthetic substrate supply and are dynamically tuned to environmental and metabolic conditions as a component of metabolic regulatory processes (Laothawornkitkul *et al.*, 2009; Lantz *et al.*, 2019; Riedlmeier *et al.*, 2017; Monson *et al.*, 2021). Due to its much higher emission rates and relative ease of detectability, isoprene has received far more study in the field, though both classes of VOC are expressed by a wide diversity of angiosperms and gymnosperms across all biomes of the globe (see Taylor *et al.*, 2021 and references therein). Within species, isoprene emission rates tend to increase toward brighter and hotter microenvironments (Niinemets, 2007), and across landscapes, emitting species increase in relative abundance toward hotter climates, exceeding half of trees in warm tropical forests (Taylor *et al.*, 2018). However, a recent study found a contrasting interspecific vertical structuring of emission capacities, with more emitting species and higher species-maximum emission rates in the mid-canopy region of an Amazonian forest (Table 2, Taylor *et al.*, 2021). Similarly, within tree crowns of European beech, monoterpene emissions were found to be highest in semi-shaded leaves beneath the canopy surface (Table 2, Šimpraga *et al.*, 2013). This pattern may indicate the importance of temporal variability in thermal conditions as distinct from the long-term average. Temperature sensitive VOC emissions have been hypothesized to enable real-time acclimation to rapidly changing leaf thermal environments typical of the mid-canopy region (see section 1, Sharkey *et al.*, 2008). Future work seeking to understand how temporal dynamics of leaf heating (see Leigh *et al.*, 2017) vary through the canopy and influence leaf function will be important for resolving the role of VOCs in forest thermal

sensitivity across the vertical gradient. Given current understanding, we may hypothesize that light-dependent VOC emissions are important for mid-canopy thermal responses, while other traits play the same role in sun-exposed canopy leaves.

5. Tree and ecosystem ecology

Differences across forest vertical gradients in biophysical conditions, plant traits, and metabolism scale up to affect tree ecology, ecosystem ecology, and their temperature responses (Fig. 1).

5.1. Tree metabolism, growth, and survival

Tree metabolism and growth are shaped by the positioning of their crowns within the vertical gradient. Tree height, crown volume, and foliage biomass all scale with diameter at breast height (DBH), which in turn is a strong predictor of tree transpiration (Anderson-Teixeira *et al.*, 2015; Meinzer *et al.*, 2001; Kunert *et al.*, 2017) and photosynthesis. Specifically, increases are linked to increased leaf area and the increasing probability that the crown is in the canopy (Muller-Landau *et al.*, 2006), where higher light availability results in higher leaf area-specific photosynthesis (Table 2). The net foliar photosynthate production is allocated among functions including respiration, above-ground woody growth, foliar turnover, root growth and allocation to root-associated microorganisms, reproduction, defense, and storage of non-structural carbohydrates (NSCs). Among these, the process about which we know the most is woody aboveground growth, which consumes only a modest fraction of total photosynthate ($\sim 1/6$ on the ecosystem level, Anderson-Teixeira *et al.*, 2021) but is disproportionately important to long-term forest dynamics and carbon cycling in that it builds up woody tissues with a long residence time in the ecosystem (Russell *et al.*, 2014). Radial stem growth may increase or decrease over time as trees grow in DBH depending on the light environment (Anderson-Teixeira *et al.* in press). In open forests and for open-growth individual trees, growth rate declines with DBH (Muller-Landau *et al.*, 2006; Anderson-Teixeira *et al.* in press), whereas growth rate consistently increases with DBH for trees established in the understory of a closed-canopy forest (Muller-Landau *et al.*, 2006; Anderson-Teixeira *et al.*, 2015). This points to a

dominant role of vertical profiles in microclimate in shaping tree growth rates within forests.

Vertical gradients also affect the climate sensitivity of metabolism and growth. Stomatal conductance tends to be more strongly limited by high atmospheric demand (high T_{air} and VPD, low RH) even before soil water becomes limited in forests not experiencing drought (Novick *et al.*, 2016; Corlett, 2011; Ruehr *et al.*, 2016). Therefore, periods of high atmospheric demand – be these on time scales of hours, days, or seasons – tend to cause greater reductions in tree transpiration and photosynthesis in tall trees that occupy canopy positions in relatively dense-canopy forests (Christoffersen *et al.*, 2016; Garcia *et al.*, 2021). This is consistent with the observation that g_s limitation with T_{air} increases with height in the canopy (Table 2). More active stomatal regulation of tall canopy trees (e.g., Mediavilla & Escudero, 2004) – often combined with greater effective rooting depth – may offset greater xylem embolism risk (Chitra-Tarak *et al.*, 2021; Olson *et al.*, 2018; Garcia *et al.*, 2021) and reduce adjustment of traits related to carbon metabolism during drought (Bartholomew *et al.*, 2020). This results in decreasing carbon isotope discrimination, indicative of an increasingly conservative hydraulic strategy, with increasing tree height (Table 1, McDowell *et al.*, 2011).

In turn, the drought sensitivity of woody growth tends to be greater in canopy trees. In the field of dendrochronology, it is generally accepted that tree ring records of large, exposed trees are best suited for climate reconstructions because their annual growth displays the greatest sensitivity to interannual variation in climate (Fritts, 1976). However, only a relatively limited number of studies have directly examined drought- or temperature-sensitivities as a function of tree size. These have most commonly found greater sensitivity to low precipitation or seasonally high temperatures among larger, more exposed trees (Fig. 4, Trouillier *et al.*, 2018; McGregor *et al.*, 2021; Gillerot *et al.*, 2020; Anderson-Teixeira *et al.* in press), corroborating evidence from globally distributed forest censuses that larger trees tend to undergo larger growth declines during drought (Bennett *et al.*, 2015). In addition to lower drought resistance of growth, larger trees frequently exhibit lower ability to recover from stress (i.e., resilience, McGregor *et al.*, 2021; Gillerot *et al.*, 2020), and greater increases in mortality (Bennett *et al.*, 2015; Stovall *et al.*, 2019). Mechanistically,

this is almost certainly driven in part by the fact that larger trees have their crowns in a microenvironment that is more challenging during drought (Figs. 1 - 3, Scharnweber *et al.*, 2019), yet there is also reason to believe that height itself provides disadvantages (Couvreur *et al.*, 2018; Olson *et al.*, 2018).

Indeed, despite the potential for shorter trees in open forests to experience greater environmental stress (Curtis *et al.*, 2019), greater drought sensitivity of larger trees has been observed in open as well as closed-canopy forests (Bennett *et al.*, 2015; Anderson-Teixeira *et al.* in press), although there is also evidence that short trees in young stands are more drought-sensitive than taller trees in mature forests (Irvine *et al.*, 2004). The relative importance of exposure versus height in shaping drought sensitivity remains to be disentangled.

While it is clear that drought sensitivity increases with crown height through forest vertical gradients, and hence with DBH, it remains unclear how growth sensitivity to high T_{air} , independent of drought, varies across this gradient. Because VPD increases rapidly with T_{air} , high T_{air} is often associated with atmospheric drought, likely explaining negative growth responses – particularly among larger trees – even if soil moisture remains high (Novick *et al.*, 2016), or when precipitation is statistically accounted for (Fig. 4, Anderson-Teixeira *et al.* in press). However, under conditions that are humid enough that canopy trees can maintain high g_s , we do not necessarily expect their photosynthesis (see section 4.2) or woody growth to exhibit higher sensitivity to T_{air} than their understory counterparts. In eight mesic forests across the northeast United States, tree-ring records showed steep growth declines of understory trees at higher T_{air} , contrasting with the responses of canopy trees (Fig 4, Rollinson *et al.*, 2020). Additional research is required to understand the mechanisms underlying these intriguing differences, and to disentangle size-related tree growth responses to hot-wet versus hot-dry conditions.

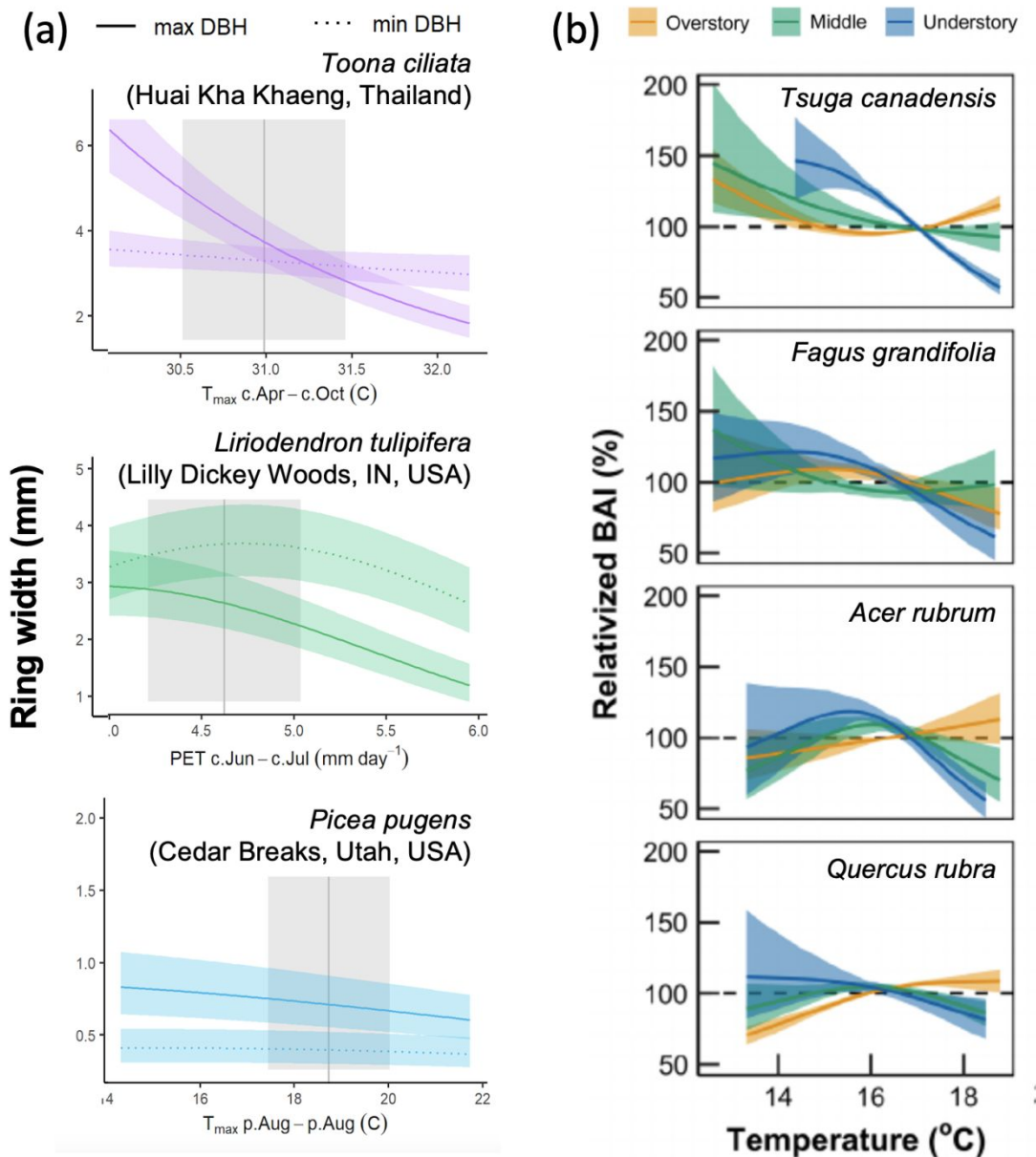
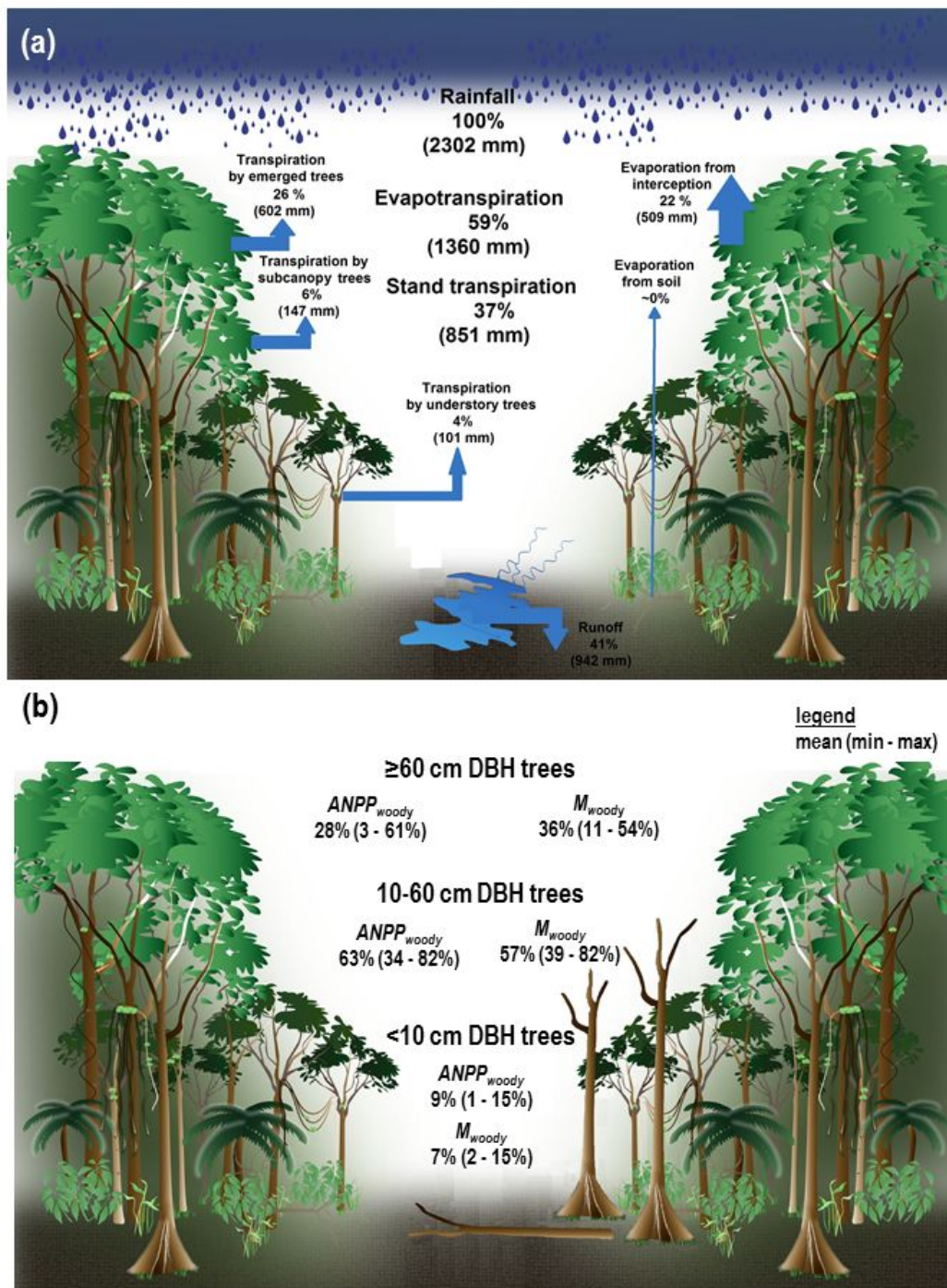


Figure 4. Examples of tree-ring analyses showing differential interannual temperature sensitivity of annual growth between large canopy versus smaller understory trees. In column (a), across three sites and species, trees with large diameter at breast height (DBH) had more negative growth responses to high temperatures during the current or previous growing season (denoted by c or p, respectively, on the x axes) than did small trees of the same species. Shown are tree ring width responses to the most influential temperature variable at the site (T_{\max} or PET) for the maximum and minimum tails of the DBH distribution included in the analysis. Colored lines represent responses to

the temperature variable in a model including a DBH - temperature interaction. Other model terms are held constant at their mean. Transparent ribbons indicate 95% confidence intervals. Vertical grey lines and shading indicate the long-term mean ± 1 standard deviation of the temperature variable. From Anderson-Teixeira *et al.* in press. In column (b), understory trees of four species had more negative growth responses to high growing season temperatures across eight New England forests. Growth is expressed as relativized basal area increment (BAI), where values $>$ and $< 100\%$ indicate higher- or lower- than-average growth, respectively. Again, colored lines indicate modeled mean temperature responses and transparent ribbons indicate 95% confidence intervals. From Rollinson *et al.* (2020).

5.2. C and water flux

Canopy trees account for the majority of forest ecosystem water and carbon cycling. While studies partitioning transpiration across forest vertical gradients are rare, both ET and transpiration have been shown to increase with height in a *Picea abies* forest in Germany, such that the upper half of the canopy contributed an estimated 80% of daytime ET (Staudt *et al.*, 2011). Similarly, in a tropical forest in the Brazilian Amazon, canopy and subcanopy trees jointly contributed approximately 93% of ET, or 88% of transpiration (Fig 5a; Kunert *et al.*, 2017), and trees >33 cm DBH contributed $>80\%$ of transpiration in a forest in Costa Rica (Moore *et al.*, 2018). In terms of C cycling, it has been estimated that canopy strata contribute $\geq 64\%$ of net daytime CO_2 uptake (i.e., GPP - ecosystem respiration, including from soil; Misson *et al.*, 2007). Large trees also dominate in terms of woody above ground net primary productivity ($\text{ANPP}_{\text{woody}}$) and mortality (M_{woody}), with trees $\geq 10\text{cm}$ DBH usually contributing $> 85\%$ of $\text{ANPP}_{\text{woody}}$ and M_{woody} across 25 globally distributed forests (Fig. 5b, Piconiot *et al.* in review).



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711 **Figure 5. Vertical partitioning of (a) evapotranspiration and (b) C fluxes in tropical forests.**

712 Panel (a) is from Kunert et al. (2017); panel (b) presents averages for 14 tropical forests from Piponiot

713 et al. in review.

It is less clear how thermal sensitivity of water and carbon fluxes vary across strata, but probable responses can be inferred based on the patterns and mechanisms reviewed above. We expect that transpiration, GPP, and $ANPP_{woody}$ should all be more sensitive to high temperatures in the upper canopy than in the understory – at least under conditions of moderate to high VPD (Grossiord *et al.*, 2020). Because canopy trees dominate these fluxes (Fig. 5), their responses will strongly influence the whole-ecosystem response, potentially with modest buffering by the understory. Thus, for example, increases in canopy T_{leaf} reduce forest GPP in the tropics (Pau *et al.*, 2018). Yet there is also evidence that GPP and ecosystem respiration are less sensitive to heat and drought stress in older forests than in young forests (Xu *et al.*, 2020), perhaps in part because of more complex vertical structuring (Jones *et al.*, 2019). A rare example of a study comparing the climate sensitivity of C fluxes across size classes (Meakem *et al.*, 2018) showed that M_{woody} was more strongly elevated among large than small trees during an *El Niño* drought in Panama, while the smallest size classes had higher productivity during the drought, likely because of increased light in the understory. It remains far less clear how thermal sensitivity varies across forest strata under wet conditions, but both physiological mechanisms (Fig. 3) and tree ring evidence (Fig. 4) suggests that understory trees may respond more negatively to hot, wet conditions. Further research is required to better understand the thermal sensitivity of forest ecosystem function across strata.

III. Implications

Having established how physical conditions and biological form and function vary across vertical gradients (Fig. 1), 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 interwoven relations between the biophysical environment and biological factors – leaf traits, metabolic processes, and distribution of species across canopy strata –

are likely to produce amplifications and feedback loops in a warming world, with implications for forests on many levels.

Warming

As climate change progresses, we anticipate increases in both mean daytime and nighttime T_{air} , as well as increased T_{max} s, with extreme increases during heat waves (IPCC, 2021). These changes will impact leaf and ecosystem gas exchange with the atmosphere, and, over longer time frames, forest structure, composition, and leaf trait distributions. Our in-depth review sheds some light as to how responses are likely to vary across forest vertical gradients, yet important uncertainties remain.

To the extent that warming is coupled to drought, we expect that the largest trees will usually be hardest-hit, particularly in cases where the drought is severe, and that this will occur at least in part because their crowns are positioned in a more challenging microenvironment (section 5.1, Figs. 1- 4, e.g., Bennett *et al.*, 2015; Stovall *et al.*, 2019; Anderson-Teixeira *et al.* in press). Specifically, warming will disproportionately stress tall canopy trees when T_{air} and accompanying VPD rise enough that sun-exposed leaves cannot maintain both hydraulic safety and the transpirational cooling required to keep T_{leaf} below damaging thresholds. In contrast, understory trees will be more sheltered during droughts and heat waves, and in some settings may benefit from increased light availability (Bennett *et al.*, 2015). An interesting open question is to what extent these patterns vary with the nature of the drought, including the relative contributions to stress from low soil moisture versus high VPD. While the two are coupled over longer time scales (Novick *et al.*, 2016; Humphrey *et al.*, 2021), the latter can be intense for short periods even when soil moisture is high (e.g., during a heat wave) and exerts a stronger influence on ET in many biomes (Novick *et al.*, 2016). Given the mechanisms reviewed here, we might expect that atmospheric dryness in particular skews the stress more towards the exposed canopy trees.

What remains poorly understood is how responses to warming will vary across vertical gradients under mesic conditions. The leaf-level responses are relatively well-understood: at the metabolic level, photosynthesis and respiration are coupled to photosynthetic

thermal optima, which reflect adaptation to the local climate but do not vary consistently with height in the canopy (see section 4.2, Table 2). Beyond this inflection point, photosynthesis declines whereas respiration continues to increase exponentially, eventually shifting the carbon balance from sink to source, independent of water and irradiance (Duffy *et al.*, 2021). While leaves display substantial plasticity to adapt to warmer temperatures (Cunningham & Read, 2003; Way, 2019; Slot & Kitajima, 2015; Slot *et al.*, 2021b) and to recover from canopy heat stress (Smith *et al.*, 2020), failure to fully acclimate will result in reduced carbon sequestration at leaf and ecosystem levels (Bennett *et al.*, 2021; Huang *et al.*, 2019; Way, 2019; Tan *et al.*, 2017). Exposed canopies are likely most vulnerable, as growing season T_{air} is increasingly equaling or exceeding photosynthetic optima (Slot & Winter, 2017; Kumarathunge *et al.*, 2019; Huang *et al.*, 2019; Mau *et al.*, 2018). Particularly in mid-latitude forests, which have the narrowest thermal safety margin between historical maximum temperatures and leaf thermal tolerance levels (O'Sullivan *et al.*, 2017), T_{leaf} of sun-exposed leaves may approach thermal tolerance thresholds during heat waves, resulting in photosynthetic decline or even leaf death (e.g., O'Sullivan *et al.*, 2017; Tiwari *et al.*, 2021; Kunert *et al.*, in press).

Although understory leaves are unlikely to face the same absolute extremes of T_{leaf} (unless exposed to sunflecks), they will also be affected by higher T_{air} , and in some ways are likely to prove more sensitive. A buffering effect from the canopies might allow shaded layers to photosynthesize longer in the day (He *et al.*, 2018; Miller *et al.*, 2021). However, with T_{air} more frequently equaling or exceeding photosynthetic optima, occasional exposure to sunflecks coupled with lower capacity to shed excess heat may prove disadvantageous. Moreover, increased nighttime T_{air} may disproportionately increase respiration relative to photosynthesis, thereby negatively affecting the carbon balance. While it is currently difficult to predict whether canopy or understory photosynthesis is likely to be more severely affected by higher T_{air} (see section 4.2), tree-ring evidence indicates that understory trees tend to exhibit greater reductions in growth during unusually hot growing seasons (section 5.1, Fig 4b, Rollinson *et al.*, 2020). Thus, while canopy trees are probably more vulnerable to mortality from distinct heat-related disturbances, such as drought or heat waves, trees in the more buffered understory may be more negatively affected by

chronic stress from warming T_{air} , which may reduce growth and increase the risk of carbon starvation in these small trees, which have lower NSC reserves (Niinemets, 2010b).

Thus, in synthesis, warming temperatures will affect trees across the vertical gradient, but the stress will be of a different nature at different heights. We expect that the tallest trees will be increasingly prone to hydraulic failure and damaging or lethal T_{leaf} 's, whereas understory trees may be increasingly prone to carbon starvation, particularly under humid conditions that make it more challenging to shed excess heat. Both groups – but probably disproportionately the canopy trees – are likely to experience increasing mortality, with the modes of mortality mirroring the current tendency for canopy trees to be more prone to climate-related disturbances including drought while understory trees are more prone to competition and carbon starvation (Gora & Esquivel-Muelbert, 2021). When the canopy trees die, this will open canopy gaps, as discussed in the following section.

Canopy disturbance

As discussed above, rising temperatures and severe droughts place the canopy trees at particularly elevated risk of mortality. Moreover, large trees are also disproportionately impacted by other climate-related disturbances (e.g., wind, lightning; Gora & Esquivel-Muelbert, 2021) that are expected to intensify with climate change (IPCC, 2021), and they are also targeted by selective logging operations (e.g., Miller *et al.*, 2011). Forest fragmentation also disproportionately kills large trees by making them more vulnerable to wind, desiccation, and liana infestation (Laurance *et al.*, 2006). Thus, canopies are becoming increasingly prone to disturbance and gap formation, which in turn increases incident radiation levels and temperatures within the canopy (Stark *et al.*, 2020). While wetter forests can prove quite resilient to such changes (Miller *et al.*, 2011), this shift to hotter and drier microclimates can often make forests more susceptible to further disturbances, for example, increasing fire risk (Brando *et al.*, 2014; Aragão *et al.*, 2018). Severe degradation impacts can cause dramatic ecological state changes (e.g., the transition from forest to more open, savanna-like vegetation in tropical forest regions through 'savannization') and non-linear threshold responses in energy balance and associated microclimates, with implications for forest-atmosphere interactions (Stark *et al.*, 2020).

Such dynamics are likely to be amplified by warming temperatures, such that climate change is pushing some of the world's forests into alternative stable states wherein forest can persist as long as the canopy remains largely intact, but has dramatically reduced probability of recovering and persisting when affected by severe canopy disturbance (Tepley *et al.*, 2017; Miller *et al.*, 2019; Stark *et al.*, 2020; McDowell *et al.*, 2020).

Canopy disturbance poses an increasing threat to the biodiversity of microrefugia that are otherwise buffered from climatic extremes (Greiser *et al.*, 2019; Scheffers *et al.*, 2013).

Canopy structure affects understory species composition, which has been shown to shift under warming and canopy disturbance (Maes *et al.*, 2020; Majasalmi & Rautiainen, 2020; Bertrand *et al.*, 2020). In the understory, warming is disproportionately affecting the less thermally-adapted plant species, resulting in associated plant community thermophilization (Greiser *et al.*, 2019; Duque *et al.*, 2015; Zellweger *et al.*, 2020). If such compositional shifts towards more thermally-adapted species fail to keep up with the pace of warming, the ecosystem-level resilience to canopy disturbance that is often provided by smaller trees (e.g., Miller *et al.*, 2011) will be destroyed, resulting in breakdown of canopy buffering and the potential state changes described above.

Scaling across space and time

As we have reviewed here, vertical profiles in forests strongly shape forest dynamics and climate change responses. Ultimately, to achieve the important goal of understanding feedbacks between the world's forests and climate change, it is essential that these mechanisms be sufficiently represented in models and scaled spatially via remote sensing.

Representing Vertical Gradients in Models

Future forest dynamics remain one of the largest sources of uncertainty in Earth system model projections of the future of global carbon cycling and climate change (Friedlingstein *et al.*, 2006). Dynamic global vegetation models (DGVMs), which comprise the land surface models in Earth system models, are used to predict the global distribution of vegetation types and biosphere-atmosphere feedbacks (Foley *et al.*, 1996; Sitch *et al.*, 2003; Woodward & Lomas, 2004). DGVMs operate at a range of scales and vary in complexity,

from detailed individual-based models (i.e., 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 spatial resolution (Shugart *et al.*, 2018), to big-leaf models that reduce 3D vegetation structure across the entire biosphere into a single vegetation layer (Bonan *et al.*, 2003; Krinner *et al.*, 2005). This simplification is computationally more efficient, although it comes at a cost of a lack of representation of important demographic processes and vertical light competition (Hurtt *et al.*, 1998; Smith *et al.*, 2001; Krinner *et al.*, 2005). The computational middle-ground to representing vertical structure in DVGs lies in cohort-based models, which represent vegetation as cohorts of individual plants, grouped together based on properties including size, age, and functional type (Fisher *et al.*, 2018). These sit between the oversimplified vegetation dynamics in big-leaf models, which do not represent any vertical stratification, and individual-based models, whose computational expense prevents them from being integrated into Earth system models.

The findings of this review reinforce the notion that representing vertical structuring, as can be done using cohort-based-models, is essential to capturing forest dynamics under global change. Improved representation of vertical variation in forest canopy architecture and ecosystem function is critical for representing thermal sensitivity and has repeatedly been identified as an important step toward reduced uncertainty and more accurate characterization of biologically mediated feedbacks (Moorcroft *et al.*, 2001; Banerjee & Linn, 2018; Bonan *et al.*, 2021). Moreover, given the anticipated importance of mid-canopy and understory trees in ecosystem resilience to increasing mortality of canopy trees, it is absolutely essential that models separately represent these strata.

A key question is whether existing models adequately represent the processes that underpin understory tree responses to thermal stress as well as large tree responses. Most models have been developed to capture dynamics in the canopy, or overstory, given the disproportionate role of these large trees in ecosystem dynamics (Fig. 5). Less attention has focused on developing and validating understory tree dynamics and responses to perturbations in models. This is likely due in large part to the fact that observational and experimental studies required to resolve key patterns and underlying mechanisms remain

somewhat sparse (see sections 4, 5). Pairing of models and observational studies will be important for further improving our mechanistic understanding of vertical gradients and their implications.

Though an improvement over big-leaf models, DGVMs 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). At the very least, multi-layered ecosystem models will likely be necessary for accurately predicting future forest function (e.g., De Pury & Farquhar, 1997; Bonan *et al.*, 2021). In addition, capturing the vertical gradients in ET, GPP, respiration, and woody growth, and subsequently the net ecosystem effects (Figs.4 - 5), requires improved characterization of the functional response of leaf-level processes (Table 2, Fig.3) to vertically varying abiotic conditions (Fig.1), and the role of traits (Table 1) in mediating responses to thermal sensitivity.

Scaling *in situ* data with remote sensing

Remote sensing data provide a valuable means to scale between *in situ* observations and DGVMs. Specifically, the increasing availability of airborne and spaceborne lidar and thermal remote sensing data offer a promising opportunity for mapping vertical thermal gradients in combination with vegetation structure at locations with *in situ* data and across larger landscapes (Fig. 6). Airborne and spaceborne lidar, as well as terrestrial laser scanning data, yield detailed 3D reconstructions of whole tree and forest structure. These data can be leveraged in combination with thermal remote sensing data from the spaceborne ECOSTRESS sensor (Hulley *et al.*, 2019; Fisher *et al.*, 2020) or drone- and tower-based Forward Looking Infrared (FLIR) cameras.

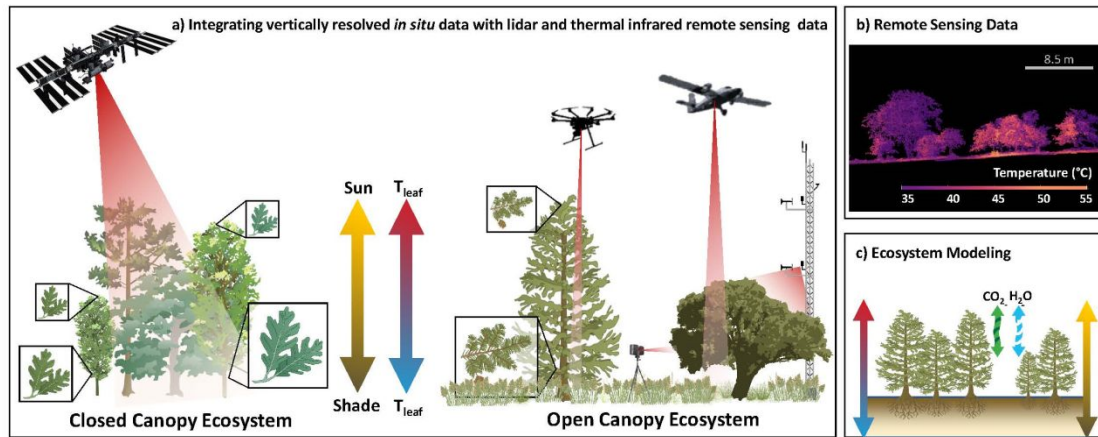


Figure 6. Lidar and thermal remote sensing data can be used to measure vertical canopy structure and plant thermal signatures at increasingly large scales. (a-b) Integrating in situ and remote sensing measurements will support our ability to scale understanding of vertical gradients within and across ecosystems. (c) In turn, these efforts can be used to directly inform ecosystem model development and parameterization. Vertically resolved in situ data could include any variable listed in Table 1 or 2. Panel b shows drone lidar point cloud data colored with thermal data from a savanna woodland in Kruger National Park, South Africa illustrating vertical and horizontal variation in vegetation temperature. Image courtesy of the Harvard Animal-Landscape Observatory, Peter B. Boucher and Andrew B. Davies.

Detailed structural information from lidar data has been used to measure tree height, DBH, and crown dimensions (Fisher *et al.*, 2020), evaluate spatial variation in vertical leaf area density profiles (Detto *et al.*, 2015), and resolve complex seasonal and diurnal variation in shortwave radiation forcing in ecosystems (Musselman *et al.*, 2013). In addition, shading by the overstory can be better represented to predict understory temperatures by modeling the time-varying interaction of the forest canopy with solar radiation, as has been done in other lidar-based analyses (e.g., Davis *et al.*, 2019b). Satellite and airborne thermal infrared remote sensing analyses are now being conducted at regional and continental scales, although very few applications exist at finer-scales necessary for understanding of vertical variation in plant canopy temperatures (Johnston *et al.*, 2020). As an example of the type of insight that can be gained from this approach, Pau *et al.* (2018) used data from a tower-based FLIR camera in combination with eddy-covariance data and found that tropical forest canopy temperatures were more strongly associated with GPP than T_{air} or VPD.

However, the authors did not consider vertical light environment conditions even though light directly influences the deviation between canopy temperature and T_{air} . In a savanna system in the western U.S., Johnston *et al.* (2020) found significant vertical variation in plant temperature, with warmer temperatures in the understory compared to the top of the blue oak canopies – a finding opposite of what was expected that occurred in association with very high grass temperatures. The growing availability of these data makes this an opportune time to link fine-scale and landscape-scale measurements with the type of *in situ* measurements reviewed above to further explore ecosystem-scale patterns in vertical temperature gradients seasonally and across biomes.

IV. Conclusions

Across vertical gradients, directional trends in the biophysical environment and leaf traits are the rule, driving variation in the physiology and ecology that have these as their underpinnings (Fig. 1). However, there remains a lot of uncertainty as to how the temperature sensitivities of metabolism and woody growth vary across these vertical gradients. The preponderance of available data suggest that while large canopy trees are the most vulnerable to warming when water is limited, understory trees may be more vulnerable under more mesic conditions, but more research is needed.

As the climate changes, patterns and processes across these vertical gradients are likely to shift as well. Under the historical temperatures to which tree species are acclimated, the canopy is an advantageous place for trees to have their crowns, as it affords higher photosynthesis and growth. However, as temperatures increase, it is likely that exposed canopy positions will become physiologically stressful for increasing proportions of time. Ensuant increased mortality of canopy trees will create an increasing number of gaps, resulting in changes to understory conditions and community composition. Ultimately, mid- and understory trees communities will be critical to the resilience of forest ecosystems under changing climate, making improved understanding and model representation of their dynamics critical to understanding future forest dynamics. Integrating the patterns and mechanisms reviewed here, along with remote sensing data on forest structure and thermal environments, into cohort-based models that integrate

with Earth system models will be critical to understanding and forecasting forest-climate feedbacks in the coming decades.

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Author Contributions

NV and KAT planned and designed the research, with contributions from all authors. NV reviewed the literature. NV, IM, EMO and MNS contributed data and analyses. All authors contributed to writing and revising of the manuscript.

Data Availability

No new data were created in this study. New analyses are based upon data available from the National Ecological Observatory Network (NEON; <https://www.neonscience.org/>). The R scripts used for new analyses are (*will be*) available via GitHub (<https://github.com/EcoClimLab/vertical-thermal-review>) and archived in Zenodo (DOI: [TBD]).

SI files

Methods S1. Methods for analyzing vertical gradients in the biophysical environment

Methods S2. Methods for leaf energy balance modeling

Methods S3. Methods for literature review

Table S1. National Ecological Observatory Network (NEON) sites included in the analysis of vertical gradients of key biophysical characteristics

986 Figure S1. Vertical gradients in micrometeorological conditions for all forested sites in the
987 National Ecological Observatory Network (NEON)
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For Peer Review

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