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

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Summary

Rising temperatures are influencing forests on many scales, with potentially strong variation vertically across forest strata. Using published research and new analyses, we evaluate how microclimate and leaf temperatures, traits, and gas exchange vary vertically in forests, shaping tree, and ecosystem ecology. In closed-canopy forests, upper canopy leaves are exposed to the highest solar radiation and evaporative demand, which can elevate leaf temperature (T_{leaf}), particularly when transpirational cooling is curtailed by limited stomatal conductance. However, foliar traits also vary across height or light gradients, partially mitigating and protecting against the elevation of upper canopy T_{leaf} . Leaf metabolism generally increases with height across the vertical gradient, yet differences in thermal sensitivity across the gradient appear modest. Scaling from leaves to trees, canopy trees have higher absolute metabolic capacity and growth, yet are more vulnerable to drought and damaging T_{leaf} than their smaller counterparts, particularly under climate change. By contrast, understory trees experience fewer extreme high T_{leaf} 's but have fewer cooling mechanisms and thus may be strongly impacted by warming under some conditions, particularly when exposed to a harsher microenvironment through canopy disturbance. As the climate changes, integrating the patterns and mechanisms reviewed here into models will be critical to forecasting forest–climate feedback.

I. Introduction

Global average temperatures have risen 1.2°C since 1900 (Rohde & Hausfather, 2020) and are expected to reach +1.5°C by 2040 (IPCC, 2021), accompanied by increasing severity and frequency of heat waves and hotter droughts (Meehl & Tebaldi, 2004; IPCC, 2021). These changes are affecting 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), causing foliar damage during heat waves (Corlett, 2011; O'Sullivan *et al.*, 2017), and reducing growth and elevating mortality during drought (McDowell *et al.*, 2020; Breshears *et al.*, 2021). The resulting feedback to climate and carbon storage, and changes in albedo and hydrology will in turn impact the future trajectory of climate change (Bonan, 2016), yet future forest dynamics remain one of the largest sources of uncertainty in Earth system model climate change projections (Friedlingstein *et al.*, 2006; Krause *et al.*, 2018; Arora *et al.*, 2020).

Future forest dynamics will depend on how climate change impacts trees of varying height and crown position. Forests are vertically stratified, and canopies moderate climatic conditions (Ozanne, 2003; Nakamura *et al.*, 2017), including buffering understory microclimates from extreme meteorological conditions (Zellweger *et al.*, 2019). Vertical gradients in biophysical variables such as temperature, light, wind, humidity, and carbon dioxide (CO₂) concentrations influence leaf temperatures, traits, and metabolism, with implications for whole-plant performance (Michaletz *et al.*, 2016; Fauset *et al.*, 2018). Although forest vertical stratification strongly influences 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 dynamics, biodiversity, energy balance, ecosystem function, and biosphere–atmosphere interactions.

Here, we review vertical gradients in the biophysical environment and plant form and function in forests, focusing on five themes (Fig. 1): the biophysical environment; leaf temperature (T_{leaf}); the leaf traits that most strongly influence T_{leaf} and thermal tolerance; leaf gas exchange and its thermal sensitivity; and, tree and ecosystem ecology. We then consider the implications for understanding forest responses to global change and how they scale across space and time.

II. Review of vertical gradients

1. The biophysical environment

The biophysical environment, defined here to include the physical structure of the vegetation and associated micrometeorological conditions, varies vertically from the forest floor to the top of the canopy (Figs 1, 2), with micrometeorological conditions largely determined by forest structure. In this section, we review the existing literature and analyze data on vegetation structure and vertical microclimate profiles from forested sites within the US National Ecological Observatory Network (NEON; Fig. 2;

Supporting Information S1; Methods S1). Although we focus 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 edge of vegetation than to height (Lowman & Rinker, 1995).

Foliage Canopy foliage is the primary physical barrier between the atmosphere and the forest floor, buffering multiple aspects of the understory conditions from large fluctuations in conditions experienced above the canopy. It strongly influences – and is influenced by – the vertical biophysical gradient. Vertical patterns in leaf area density (i.e. leaf area per unit volume) differ across forests (Figs 2a,b, S1). In tropical and temperate forests with dense broadleaf canopies, leaf area density is generally highest in the canopy layer (i.e. that formed by the crowns of dominant trees), but understory leaf area density is often high as well, sometimes causing undulating patterns with height (Parker *et al.*, 1989; Ashton & Hall, 1992; Koike & Syahbuddin, 1993; Domingues *et al.*, 2005). In forests with more open upper canopies, including many needleleaf forests, leaf area density can be greatest in the lower canopy or understory (Baldocchi *et al.*, 1997; Law *et al.*, 2001; Bonan, 2016; Hanberry *et al.*, 2020). Soil moisture conditions, topography, and gap formations following disturbances all alter foliage patterns (Stark *et al.*, 2012; de Almeida *et al.*, 2016; Bonan, 2016; Hanberry *et al.*, 2020). In addition, seasonally dry and wet conditions, deciduousness, and phenology contribute to temporally shifting leaf area density patterns (Tang & Dubayah, 2017; Parker *et al.*, 2019; Smith *et al.*, 2019; Nunes *et al.*, 2022). In this review, we focus on growing season conditions unless otherwise noted.

Light The intensity of visible and photosynthetically active radiation (PAR, 400–700 nm) decreases from the canopy top to the forest floor, with a profile whose shape is modified by leaf area density, leaf clumping, canopy height, and vertical structure across species and forest types (Figs 2d, S1; Koike *et al.*, 2001; Béland & Baldocchi, 2021; Bin *et al.*, 2022). Canopy foliage absorbs a large portion of PAR (400–700 nm) and selectively filters light, thereby altering the spectrum of PAR received in the lower canopy and understory layers. The ratio of red (c. 685–690 nm) to far red (c. 730–740 nm) light declines along with total PAR with increasing depth in the canopy, and understories receive diffuse light enriched in near-infrared radiation (700–1000 nm; de Castro, 2000; Poorter *et al.*, 2000). Midcanopies and understories experience a highly dynamic light environment due to sunflecks, or brief increases in direct solar radiation, caused by small canopy gaps, wind-induced canopy movements, or the sun's passage across a dynamically structured canopy surface (Way & Pearcy, 2012). This light gradient is more pronounced in dense canopies, including broadleaf and mixed forests, than in forests with more open upper canopies, including many conifer forests (Figs 2d, S1; Chazdon & Fetcher, 1984; Baldocchi *et al.*, 1997; Bartemucci *et al.*, 2006; Tymen *et al.*, 2017; Parker *et al.*, 2019). This light gradient drives variation in leaf temperature (Section II.2), traits (Section II.3), and photosynthesis (see Section II.4, subsection 'Photosynthesis').

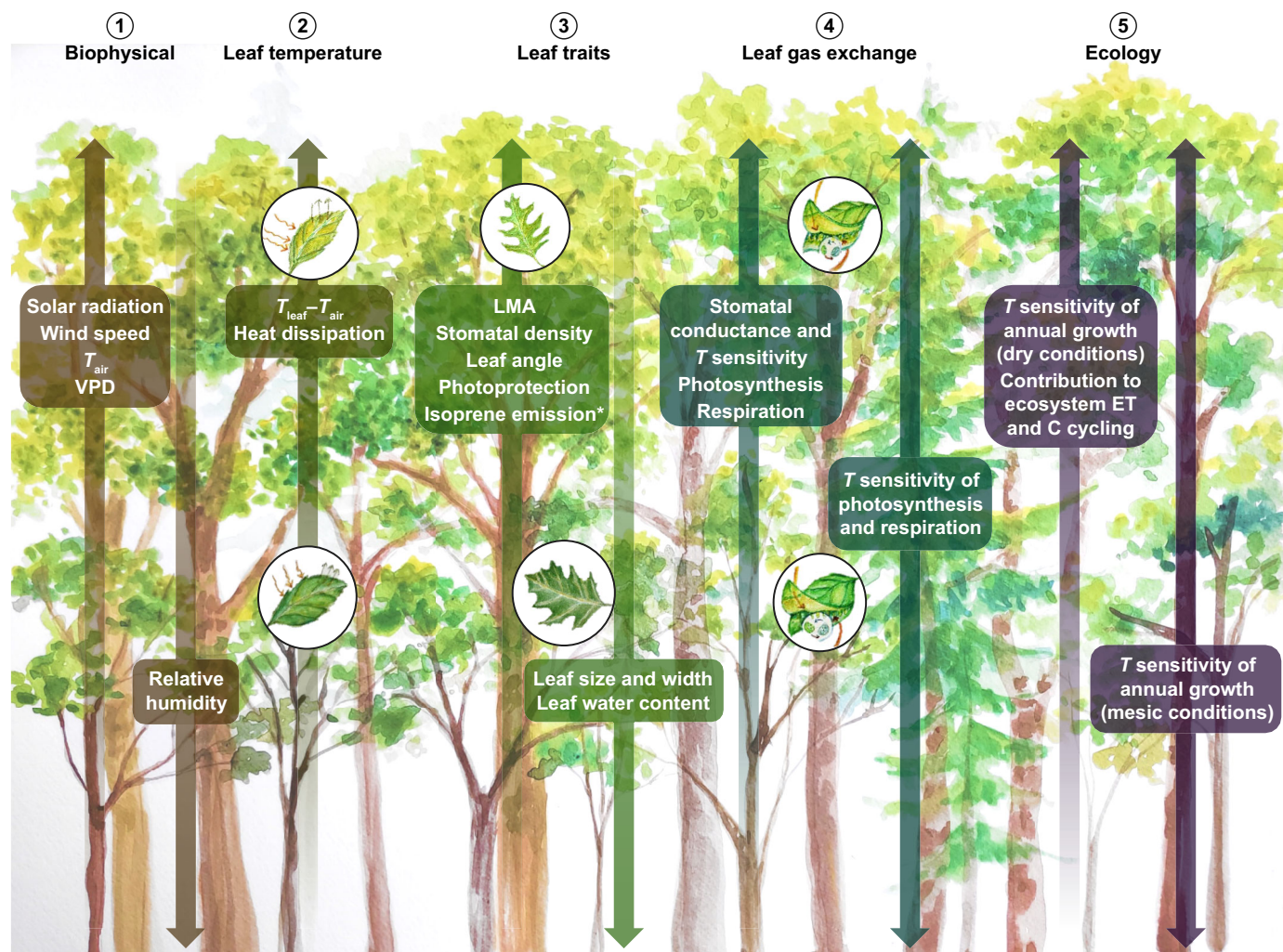


Fig. 1 Schematic summarizing typical vertical gradients in (1) biophysical environment, (2) leaf temperature (T_{leaf}), (3) leaf traits, (4) leaf gas exchange, and (5) tree and ecosystem ecology within closed-canopy forests during daytime growing season conditions. Arrows indicate direction of increase, with double-pointed arrows indicating that the direction of the trend is uncertain or inconsistent. Patterns tend to be weaker, or sometimes reversed, in more open forests, when canopy trees are seasonally deciduous, or at nighttime. ET, evapotranspiration; LMA, leaf mass per area; T sensitivity, temperature sensitivity; T_{air} , air temperature; $T_{\text{leaf}} - T_{\text{air}}$, leaf-to-air temperature difference; VPD, vapor pressure deficit. *Isoprene emission has also been observed to peak in midcanopy (Table 1).

Turbulent transport and wind Vertical transport in forest canopies is dominated by turbulent transport, making vertical profiles of wind speed, water vapor, CO_2 , and temperature more difficult to predict and to generalize on the basis of theoretical first principles than radiation profiles. Above the canopy, turbulent transport typically mimics diffusion – that is, vertical fluxes of heat, mass, and momentum are proportional to their respective vertical gradients, and to transfer coefficients (eddy diffusivities; Penman & Long, 1960) – such that wind speed declines logarithmically with proximity to the canopy surface (Monteith & Unsworth, 2013). Interaction with a plant canopy also attenuates wind, causing wind speed to decline through the canopy, for example, small plant elements can rapidly dissipate momentum within dense canopies (Raupach & Shaw, 1982; Baldocchi & Meyers, 1988). Within canopies, however, transport often fails to mimic diffusion – for example, transport of momentum (Shaw, 1977) or heat

(Raupach, 1987) may occur in the direction opposite to that predicted by gradients of wind speed or temperature, respectively – making vertical wind profiles difficult to generalize from first principles (Denmead & Bradley, 1987; Meyers & Paw, 1987; Raupach, 1989; Katul & Albertson, 1999; Harman & Finnigan, 2007). Such counter-gradient transport may arise from the intermittent generation, at the canopy surface, of large wakes or coherent eddy structures that periodically dip down through the canopy, gathering packets of warmed, humidified, and CO_2 -enriched or depleted air from beneath and within the canopy and flushing them to the atmosphere above (Finnigan, 1979; Baldocchi & Meyers, 1991). These ‘sweep-eject’ events can couple understory conditions more directly to conditions above the canopy than beneath.

Despite these complexities of within-canopy transport, wind speeds are generally much higher at the top of the canopy than

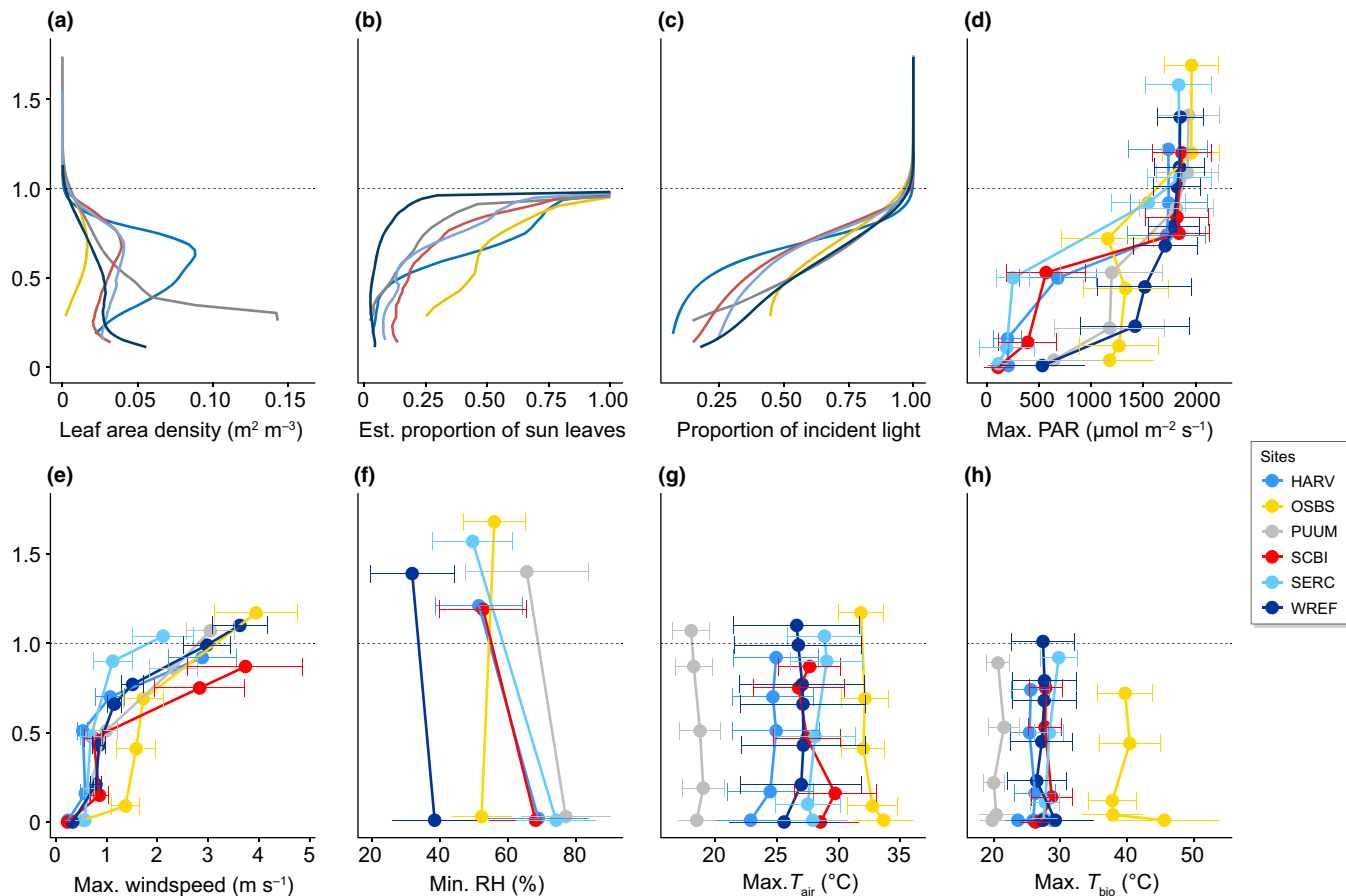


Fig. 2 Vertical gradients in the biophysical environment for six USA forest sites in the National Ecological Observatory Network (NEON). Height profiles, normalized relative to the top of the canopy, are shown for: growing season (a) modeled leaf area density, (b) estimated proportion of sun leaves, and (c) proportion of light incident to the top of the canopy (as fraction relative to top of canopy), and for July mean \pm 1 SD 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 (normalized height = 0 m) to the top of the canopy (horizontal dashed line at normalized height = 1) or above (d–g). Variables shown in (a–c) are derived from LiDAR, and those shown in (d–h) from micrometeorological tower data. 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 Methods S1. Vertical profiles in micrometeorological variables (d–h) at all forested NEON sites are shown in Fig. S1.

within or beneath (Jiao-jun *et al.*, 2004; Jucker *et al.*, 2018). This holds true across the range of forest types (Figs 2e, S1; Barnard & Bauerle, 2016; Hanberry *et al.*, 2018, 2020; Jucker *et al.*, 2018; Muller *et al.*, 2021) and savannas (Curtis *et al.*, 2019; Johnston *et al.*, 2022). As a result, upper canopy leaves have substantially higher boundary layer conductance (g_b) and therefore greater potential for exchange of both mass and sensible heat exchange (Sections II.2 and the II.4 subsection 'Conductance').

Atmospheric concentrations of CO₂ and water vapor Atmospheric CO₂ concentrations tend to be higher near the ground at night, associated with plant and soil respiration, but the elevated CO₂ quickly dissipates during the day such that CO₂ concentration differences are negligible for most of the day when photosynthesis is occurring (Brooks *et al.*, 1997; Yang *et al.*, 1999; Koike *et al.*, 2001). While understory seedlings may benefit modestly from higher CO₂ concentrations near the ground during some parts of the day (e.g.

6% of C fixation from recently respired CO₂; Brooks *et al.*, 1997), gradients in CO₂ concentrations likely have little effect on energy balance and metabolism of trees across the vertical gradient (Brooks *et al.*, 1997).

Relative humidity (RH) tends to be higher in the understory and decreases with height, although this trend is absent in open forests (Figs 2f, S1; Jucker *et al.*, 2018; Bin *et al.*, 2022). 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 air temperature T_{air} and T_{leaf} RH determines leaf-to-air 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; Tymen *et al.*, 2017; Fauset *et al.*, 2018). Especially when canopy height and leaf area index (LAI) are large, maximum T_{air} and VPD are reduced in the understory (Jucker *et al.*, 2018). The

implication is that upper canopy leaves have higher g_s and associated potential for water and heat loss than understory leaves (Sections II.2 and the II.4 subsection 'Conductance').

Air temperature Vertical gradients in air temperature (T_{air}) vary widely (Figs 2, S1), depending on factors such as vegetation type, local topography, vertical air mixing, cloud cover, sensible heat emissions, and times of day and year (Zellweger *et al.*, 2019; De Frenne *et al.*, 2021). Commonly, attenuation of radiation and vertical transport of sensible heat by the canopy buffers the lower canopy and understory from large diel and seasonal swings in air temperature (Zellweger *et al.*, 2019; De Frenne *et al.*, 2021; Haesen *et al.*, 2021). Diel temperature range is typically smaller beneath dense canopies than above, resulting from lower maximum daytime T_{air} and warmer nighttime minimum T_{air} than beneath open canopies or in nearby clearings (von Arx *et al.*, 2012; Zellweger *et al.*, 2019; De Frenne *et al.*, 2021). Notably, buffering against high maximum daytime T_{air} becomes weaker and can be reversed as canopies become more open (Fig. S1; Curtis *et al.*, 2019; Meeussen *et al.*, 2021). Analogous to a 'canopy greenhouse effect', in open forests, below-canopy maximum T_{air} can be warmer than canopy T_{air} , due to turbulent air mixing and interception of thermal radiative flux from the soil and the canopy by lower canopy layers (e.g. OSBS, Figs 2g, S1b; Banerjee *et al.*, 2017; Curtis *et al.*, 2019; Muller *et al.*, 2021). These usually modest gradients in T_{air} combine with the above-described gradients in micrometeorological conditions to shape T_{leaf} patterns within canopies.

2. Leaf temperature

T_{leaf} is strongly tied to, and usually within a few degrees of, T_{air} (Rey-Sánchez *et al.*, 2016; Drake *et al.*, 2020) but can be substantially warmer or cooler under certain conditions (Notes S1; Doughty & Goulden, 2008; Vogel, 2009; Rey-Sánchez *et al.*, 2016). Deviation of T_{leaf} from T_{air} is influenced by other micrometeorological drivers and by leaf traits and stomatal conductance (g_s ; Fig. 3; Notes S1), all of which vary across forest vertical gradients (Fig. 1). High radiation in the upper canopy implies that upper canopy leaves often have higher $T_{\text{leaf}} - T_{\text{air}}$ and thus are often warmer than understory leaves (Fig. 3a). However, higher wind speeds reduce $T_{\text{leaf}} - T_{\text{air}}$ (Fig. 3b; Niinemets & Valladares, 2004; Bonan, 2016). In addition, adaptive leaf traits that increase g_s and g_b , such as small size and high stomatal density (Notes S1; Sections II.3 and II.4 subsection 'Conductance'), mediate the direct effects of solar radiation on upper canopy leaves and result in higher rates of heat loss (Fig. 3b–e). By contrast, in the lower canopy, greater RH (reduced VPD) and lower wind speeds (reduced g_b) may limit leaf cooling via latent heat flux, increasing T_{leaf} (Tibbitts, 1979; Perez & Feeley, 2018). Leaves in these normally shaded locations can experience rapid light and temperature surges during sunflecks ($> 10^\circ\text{C}$; Way & Pearcy, 2012).

Elevation of T_{leaf} above T_{air} varies with micrometeorological conditions. During drought (associated with conditions that are hot and dry, with higher-than-average solar radiation), when g_s is limiting, $T_{\text{leaf}} - T_{\text{air}}$ will tend to be higher in the upper canopy than in the understory (Fig. 3). This is because sun leaves are exposed to

higher irradiance and VPD and therefore have stronger g_s limitation than shade leaves (Fig. 3e; Leigh *et al.*, 2017; Fauser *et al.*, 2018). By contrast, under conditions conducive to stomatal opening, higher wind speeds and g_b enable cooling in the upper canopy, whereas lower wind and g_b in the understory limit evaporative cooling (Fig. 3b,d; Roberts *et al.*, 1990; Martin *et al.*, 1999; Leigh *et al.*, 2017). Thus, while understory and within-canopy shade leaves can remain cooler under lower radiation, their environment is less conducive to dissipating excess heat compared with upper canopy leaves, because wind speeds and hence g_b are generally smaller in the lower canopy (Roberts *et al.*, 1990; Martin *et al.*, 1999). Limitations in heat dissipation in shade leaves, together with physiological propensities, may cause above-optimal T_{leaf} under slight heat or drought stress or during sunflecks (Schymanski *et al.*, 2013; Leigh *et al.*, 2017; Song *et al.*, 2020). In addition to lower wind speeds, higher RH (lower VPD) in the understory and inner canopy also reduces evaporative cooling (because evaporation rate generally increases with VPD), thus increasing $T_{\text{leaf}} - T_{\text{air}}$ (Fig. 3c; Tibbitts, 1979; Dietz *et al.*, 2007; Perez & Feeley, 2018; Song *et al.*, 2020; Konrad *et al.*, 2021).

Vertical T_{leaf} gradients also vary with canopy structure (Figs 2h, S1). Forests with closed canopies and high LAI, including tropical and temperate broadleaf forests, act as a parasol, absorbing most incoming radiation and preventing vertical air mixing in the understory. Therefore, in these forests, leaves in the upper canopy can experience greater $T_{\text{leaf}} - T_{\text{air}}$ and higher maximum T_{leaf} than lower canopy leaves, in some cases exceeding photosynthetic temperature optima (T_{opt}) because of g_s limitation and high radiation (Doughty & Goulden, 2008; Mau *et al.*, 2018; Carter *et al.*, 2021; Miller *et al.*, 2021). By contrast, open canopies with lower LAI allow more vertical air mixing and sunlight into the understory, which can either neutralize a T_{leaf} gradient or elevate $T_{\text{leaf}} - T_{\text{air}}$ at lower heights relative to the upper canopy (Martin *et al.*, 1999; Zweifel *et al.*, 2002; Muller *et al.*, 2021). The latter can result from a combination of still air at lower heights, sunflecks or the 'canopy greenhouse effect' (see Section II.1 subsection 'Air temperature'), and the tendency for shade leaves to have lower g_s (Section II.3; Schymanski *et al.*, 2013; Hardwick *et al.*, 2015). Similarly, in very open forests or savannas, trees growing close to the ground can experience greater heat stress in their lower-than-upper canopies due to the heat from the soil increasing T_{leaf} near the ground (Hadley & Smith, 1987; Curtis *et al.*, 2019; Johnston *et al.*, 2022). One of the few 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 vertical profile of a dense subalpine stand in the alpine Eastern Swiss Alps (Webster *et al.*, 2018). However, the opposite trend was observed for a lone tree surrounded by grass in a California open oak woodland, with cooler temperatures at the top of the crown, indicating a strong influence of closed-canopy shading on vertical temperature gradients (Johnston *et al.*, 2022).

3. Leaf traits

Anatomical, structural, and biochemical leaf traits vary vertically across forest strata (Table 1; Sack *et al.*, 2006; Niinemets

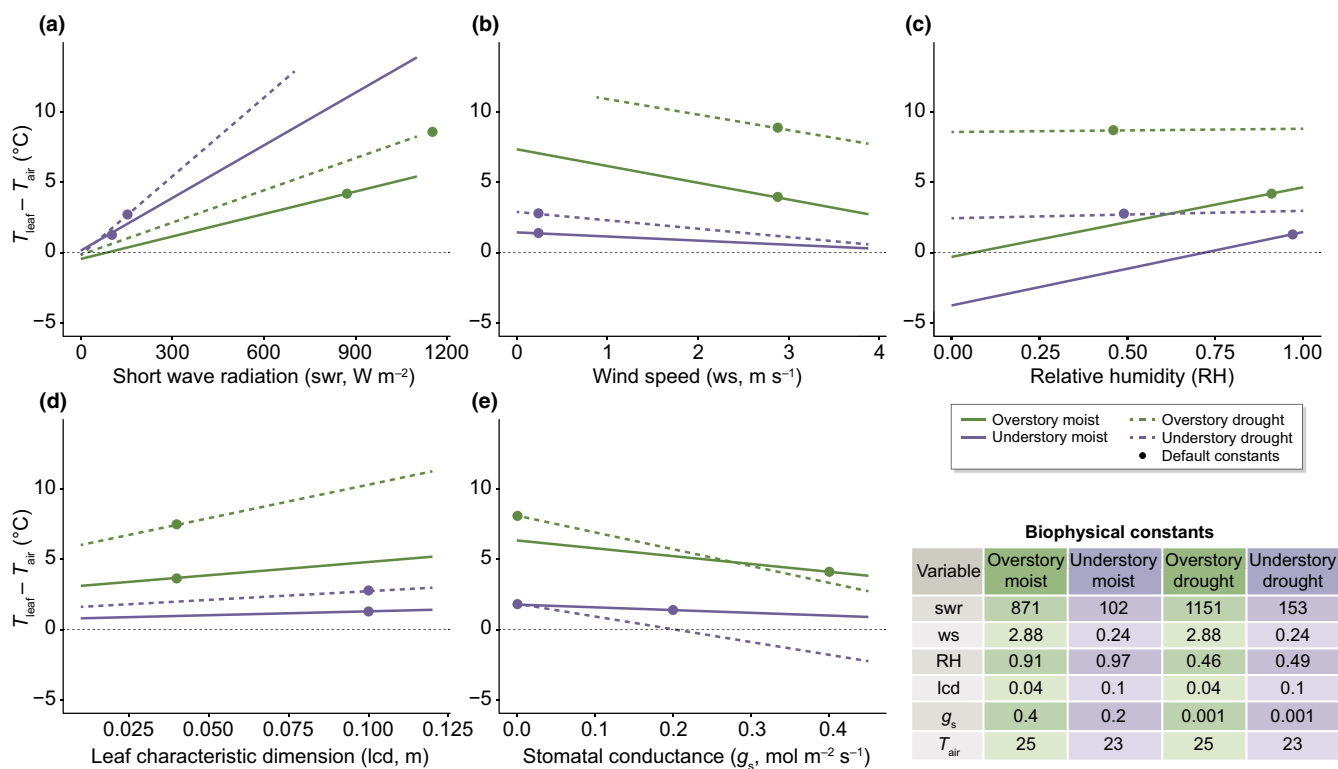


Fig. 3 Theoretical expectations for variation in the difference between leaf and air temperatures, $T_{leaf} - T_{air}$, in response to (a) shortwave radiation, (b) wind speed, (c) relative humidity (RH), (d) leaf characteristic dimension, and (e) stomatal conductance. Leaf temperatures were modeled using the TEALEAVES R package of Muir (2019) parameterized to represent a broadleaf species (*Quercus rubra*) in a mesic temperate forest (Harvard Forest, MA, USA) under hypothetical moist and drought conditions, as detailed in Supporting 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. Dots along each line correspond to the biophysical constant assigned for the independent variable in the other scenarios, and therefore represent the modeled value for $T_{leaf} - T_{air}$ with all parameters set to the biophysical constants given in the table. Biophysical constants in the table include the following: shortwave radiation (swr), wind speed (ws), relative humidity (RH), leaf characteristic dimension (lcd), stomatal conductance (g_s), and air temperature (T_{air}).

et al., 2015a; Chen *et al.*, 2020), shaping vertical profiles of leaf temperature, gas exchange, and thermal sensitivity (Zwieniecki *et al.*, 2004; Michaletz *et al.*, 2015, 2016). Vertical variation in leaf structure and composition has long been recognized, with sun and shade leaf traits distinguished for over a century (Haberlandt, 1914; Salisbury, 1928). Early work attributed differences among leaves to sun vs shade (Wylie, 1951; Vogel, 1968), and this tendency grew given the parallel differences observed for plants grown in sun vs shade (Boardman, 1977; Abrams & Kubiske, 1990). More recent work has extended the focus from light alone to height in the vertical profile, as the latter shapes differences in leaf structure and function that can partially mitigate the effects of gravity and hydraulic pathlength on leaves higher up in the canopy (Koch *et al.*, 2004; Burgess *et al.*, 2006; Sack *et al.*, 2006). For example, leaf mass per area (LMA), photosynthetic capacity (A_{max} per area), and g_s have been observed to increase with height, independently of light (Cavender-Bares & Bazzaz, 2000; Thomas & Winner, 2002; Houter & Pons, 2012; Bin *et al.*, 2022). Thus, leaves develop differently according to the irradiance and hydraulic stress associated with their canopy location, height, and evaporative load, with additional potential influences of branch ontogenetic stage (Sack *et al.*, 2006; Niinemets, 2010; de Casas *et al.*, 2011;

Niinemets *et al.*, 2015b; Keenan & Niinemets, 2016; Chen *et al.*, 2020; Carter *et al.*, 2021; Bin *et al.*, 2022). Plasticity throughout the canopy may emerge when development of new leaves is influenced by information from adjacent mature leaves or apical meristems and may also acclimate during and after expansion to the current microclimate (Zwieniecki *et al.*, 2004). Overall, leaf biochemistry, anatomy, and structure may be optimized to local conditions (Niinemets, 2007; Lloyd *et al.*, 2010; Hikosaka, 2014; Kitao *et al.*, 2012; Buckley, 2021). However, we lack a cohesive framework for integrating the many differences in leaf traits throughout the canopy. Rather, much of our understanding of trait coordination is based on the leaf economics spectrum concept developed across diverse species using sun leaves (Wright *et al.*, 2004; Keenan & Niinemets, 2016; Chen *et al.*, 2020). As canopy shade is known to alter these trait relationships (Osnas *et al.*, 2018), further research is needed to characterize trait relationships and responses vertically through the full range of canopy microenvironments.

Across the vertical gradient, traits vary: (1) within individuals, across height and light gradients (Zwieniecki *et al.*, 2004; Sack *et al.*, 2006; Bin *et al.*, 2022); (2) across individuals of the same species, often representing an ontogenetic trajectory from the

understory to the canopy (Niinemets, 2010; Carter *et al.*, 2021); and, (3) among understory and canopy species (Lloyd *et al.*, 2010). Most 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). Generally, the pattern of fundamental trait adaptations to light gradients across forest species is similar to within-species trends (Thomas & Winner, 2002; Rozendaal *et al.*, 2006; Cavaleri *et al.*, 2010; Lloyd *et al.*, 2010; Houter & Pons, 2012; Bin *et al.*, 2022); however, vertical trends vary across trees (Lloyd *et al.*, 2010), and counter-gradient variation can exist (Lusk *et al.*, 2008). Many leaf physiological parameters can be estimated based on foliage height profiles (Cavaleri *et al.*, 2010; Lloyd *et al.*, 2010).

Leaf anatomy and morphology Sun leaves have anatomical, morphological, and physiological traits that reduce T_{leaf} through higher conductance (g_s or maximal g_s) and/or reflectance (Table 1). Thus, sun leaves are generally smaller and thicker, with higher LMA, and are more deeply lobed (Fig. 3; Vogel, 1968; Zwieniecki *et al.*, 2004; Sack *et al.*, 2006; Leigh *et al.*, 2017), but with greater leaf packing and clumping (which reduces g_s). Steeper leaf angles reduce midday radiation loads and thereby decreasing $T_{\text{leaf}} - T_{\text{air}}$ (Ball *et al.*, 1988; Niinemets, 1998), while higher trichome density increases reflectance, also decreasing radiation load. Furthermore, sun leaves tend to have higher stomatal and vein densities, which facilitate evaporative cooling by enabling higher g_s (see Section II.4 subsection 'Conductance'; Zwieniecki *et al.*, 2004). Yet, sun leaves also have adaptations to limit water stress, particularly in drier climates, including greater cuticle thickness and higher trichome density (which may reduce or increase g_s ; Schreuder *et al.*, 2001; Ichie *et al.*, 2016). By contrast, shade leaves have traits that maximize light capture (e.g. lower LMA and greater light absorptance per unit biomass), but larger leaves and lower transpiration make them more prone to overheating than sun leaves (de Casas *et al.*, 2011; Schymanski *et al.*, 2013; Leigh *et al.*, 2017). In open canopies, where light is comparatively homogeneous, leaf traits may be shaped more by maximum T_{air} and VPD stress than by light (Mediavilla *et al.*, 2019).

Leaf optical properties Leaf optical properties are influenced by anatomical, morphological, and biochemical traits that vary throughout the canopy (see Section II.3 subsections 'Leaf anatomy and morphology' and 'Metabolic capacity and efficiency'). High in the canopy, high light absorptance can lead to photoinhibition and would, in part, be mitigated by T_{leaf} regulation (see Section II.3 subsections 'Biochemical protection against foliage light and heat damage' and 'Thermal tolerance'; Table 1). For leaves in higher light environments, light absorptance and thus heat load can be reduced by leaf surface modifications (e.g. trichomes and cuticle) that increase reflectance, and heat may be dissipated biochemically by carotenoids, including xanthophylls (Table 1; Lee *et al.*, 1990; Knapp & Carter, 1998). Furthermore, sun leaves tend to be thicker, with more palisade layers, which act as 'light pipes' that channel abundant light into deeper cell layers, enhancing photosynthetic capacity (Lee *et al.*, 1990; Poorter *et al.*, 1995). By contrast, shade leaves have lower LMA and absorb more light per

unit mass investment, as well as denser chloroplast layers and a greater proportion of spongy mesophyll, more effective for capturing diffuse light (Table 1; Lee *et al.*, 1990; Poorter *et al.*, 1995, 2000).

Metabolic capacity and efficiency Most leaf biochemical traits also vary across light and height gradients (Table 1), both shaping and resulting from gradients in metabolism (Section II.4). Sun leaves have higher area-based concentrations of elements such as nitrogen (N_{area}) and phosphorus (P_{area}) that are critical for respiration (Meir *et al.*, 2001; Weerasinghe *et al.*, 2014) and photosynthesis (Niinemets & Valladares, 2004; Weerasinghe *et al.*, 2014; Scartazza *et al.*, 2016). Increases in chlorophyll *a/b* ratios with height reflect greater light availability in the upper canopy, while greater chlorophyll concentrations at lower heights increase PAR absorptance efficiency of shade leaves (Table 1). Higher photosynthetic rates (area based) and more frequent stomatal closure in sun-exposed canopies (Section II.4) reduce intercellular CO_2 concentrations and increase leaf $\delta^{13}\text{C}$ (Table 1).

Biochemical protection against foliage light and heat damage Biochemical protection against light and heat damage increases with peak radiation loads and thus tends to be higher in the upper canopy, which is subject to higher T_{leaf} and hydraulic limitations, than in the understory (Table 1). More frequent stomatal closure in upper canopy leaves (Section II.4) reduces their capacity to use light energy for photochemistry, thereby requiring a high capacity to dissipate excess light energy and protect against photoinhibition (Niinemets, 2007). Accumulation of excess light energy causes overreduction of the electron transport chain and the formation of harmful reactive oxygen species (Niyogi, 2000; Suzuki & Mittler, 2006). A ubiquitous defense is a rapidly inducible nonphotochemical quenching (NPQ) mechanism that responds to the increased thylakoid pH gradient caused by excess light (Niyogi, 2000; Goss & Lepetit, 2015). This form of NPQ entails interconversion of xanthophyll cycle pigments – violaxanthin, antheraxanthin, and zeaxanthin (VAZ) – which regulates the capacity for de-excitation of chlorophyll through thermal dissipation instead of photochemistry. Leaves in higher light environments show a greater capacity for NPQ and higher concentrations of VAZ as well as other carotenoids (e.g. beta carotene and lutein) employed as antioxidant defenses (Table 1; Niinemets *et al.*, 1998; García-Plazaola *et al.*, 2004; Scartazza *et al.*, 2016). By contrast, to maximize photosynthesis and minimize damage during T_{leaf} surges caused by sunflecks (Section II.2), shade-acclimated leaves tend to induce photochemical processes more quickly (Urban *et al.*, 2007) and also show a steeper response of NPQ to light than sun-acclimated upper canopy leaves (Scartazza *et al.*, 2016).

Heat-sensitive, light-dependent (photosynthetically linked) emissions of volatile organic compounds (VOCs), including isoprene and monoterpenes, enhance photosynthetic thermal tolerance by regulating antioxidant defenses and other metabolic processes (Copolovici *et al.*, 2005; Sharkey *et al.*, 2008; Vickers *et al.*, 2009; Riedlmeier *et al.*, 2017; Taylor *et al.*, 2019; Monson *et al.*, 2021). In contrast to VOCs stored in oils that are released passively by heat and wounding, such as the monoterpenes

Table 1 Summary of typically observed variation in leaf traits and its thermal sensitivity across the vertical gradient and/or between sun and shade leaves.

Trait	Symbol	Units	Response ¹	Forest type(s) ²	Reference(s) ³
Leaf anatomy and morphological traits					
Leaf area	LA	cm ²	↓ H ↓ L	TrB, TeB, BoN TrB, TeB, BoN	7, 8, 10 7, 8, 3, 10
Leaf mass per area (or inverse of specific leaf area)	LMA (or 1/SLA)	g cm ⁻²	↑ H ↑ L	TrB, TeB, TeN, BoN TrB, TeB, TeN, BoN	1, 55, 64, 7, 2, 3, 4, 6 1, 7, 2, 3, 5, 6
Leaf thickness		μm	↑ H ↑ L	TrB, TeB, TeN TrB, TeB, TeN	15, 11, 2, 13, 16 11, 15, 2, 5
Leaf density		g cm ⁻³	↑ H ↑ L	TeB TrB, TeB	2 6, 2
Pinnate lobation		cm ²	≈ L ↑ H ↓ H ↑ L	TeN TeB TeB TeB	5 3 8 8, 3
Leaf packing		n cm ⁻¹ stem	↑ L	TeN	25, 26
Blade inclination angle (vertical)	φB	°	↑ H ↑ L	TrB, TeB TrB, TeB	21, 22, 23 21, 24, 23, 22, 48
Trichome density		mm ⁻²	↑ H ↑ L	TrB TrB, TeB	17 17, 18, 19, 20
Stomatal density	D_{stomata}	mm ⁻²	↑ H ↑ L	TrB, TeB, TeN TrB, TeB	11, 12, 3, 13, 4 12, 11, 3
Total vein density	VLA	mm mm ⁻²	↑ H ↑ L	TeB TeB	46 46, 47
Minor vein density	VLA _{min}	mm mm ⁻²	↑ H ↑ L	TeB TeB	14 14, 47
Upper cuticle thickness	CT	μm	↑ H ↑ L	TrB, TeN TrB, TeB	27, 4 27, 28
Leaf optical properties					
PAR absorptance		%	≈ ↑ H ≈ ↑ L	TrB TrB	42, 45 42, 45
Absorptance efficiency per unit biomass		% g ⁻¹	↓ H ↓ L	TrB TrB	42, 45 42, 45
PAR transmittance		%	↓ H ↓ L	TrB TrB	42, 45 42, 45
Reflectance		%	≈ H ↑ H ≈ L	TrB BoN TrB	42, 45 6 42, 45
Traits related to metabolic capacity and efficiency					
Nitrogen content	N	g m ⁻² mg g ⁻¹	↑ H ≈ ↓ H ≈ ↓ L	TrB, TeB, TeN, BoN TrB, TeB, TeN TrB, TeB, TeN	55, 64, 7, 29, 30, 32, 31, 9 55, 15, 7, 29, 30, 32, 34 7, 35, 29, 30, 32, 5
Phosphorus content	P	g m ⁻² mg g ⁻¹	↑ H ↑ L ≈ L ≈ ↓ H ≈ L	TrB, TeB, TeN TrB, TeB, TeN TrB, TeB TrB TrB, TeB	55, 15, 36, 1, 37 15, 5 1 55, 15, 35, 1 15, 35, 1
Chlorophyll content	Chl	mg cm ⁻²	↓ H ↓ L	TrB, TeB TrB, TeB	40, 41 42, 41
Chlorophyll a/b ratio	chl a/b	mol mol ⁻¹	↑ H ↑ L	TrB, TeB, BoN TrB, TeB, BoN	42, 30, 6 42, 30, 39, 22, 6
Carbon isotope ratio	δ ¹³ C	‰	↑ H ↑ L	TrB, TeB, TeN TrB, TeB, TeN	55, 64, 7, 43, 31 7, 29, 31
Intercellular CO ₂ concentration	C _i	μmol mol ⁻¹	↓ H ↓ L	TeB, BoN TeB	51, 30, 44 30, 44
Biochemical protection against light and heat damage					
β-Carotene and lutein		μmol m ⁻²	↑ H ↑ L	TrB, TeB, BoN TrB, TeB, BoN	30, 42, 6 30, 38, 6
Xanthophyll cycle pigments	VAZ	μmol m ⁻²	↑ H ↑ L	TrB, TeB TrB, TeB	38, 30, 22 39, 30
Abundance isoprene emitters		%	↑ H (peak in mid-canopy) ↑ L	TrB TeB	49 50

Table 1 (Continued)

Trait	Symbol	Units	Response ¹	Forest type(s) ²	Reference(s) ³
Isoprene emission rate	<i>I</i>	nmol m ⁻² s ⁻¹	↑ H (peak in mid-canopy)	TrB	49
			↑ H	TeB	32, 60
			↑ L	TeB	32, 61, 62
Monoterpene emission rate	MT	μg m ⁻² s ⁻¹	↑ H (peak in mid-canopy)	TeB	63
Thermal tolerance					
Photosynthetic heat tolerance	<i>T</i> ₅₀	°C	↓ H ⁴	TrS	52
			≈ ↑ L	TrB, TeB	53, 54
Critical temperature beyond which <i>F</i> _v / <i>F</i> _m declines	<i>T</i> _{crit}	°C	≈ ↑ L	TrB, TeB	53
Phenology					
Budbreak		day of year	↓ H	TeB	56
Leaf life span		months	↓ H	TrB	57
			↓ L		
Drought deciduous leaf habit		%	↑ H	TrB	58, 59

Studies listed here were compiled using a systematic review process, as described in Supporting Information Methods S3.

¹Responses 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). ≈ indicates lack of any notable directional variation, and ≈ ↑ or ≈ ↓ indicate nonsignificant or mixed trends (e.g. significant in some but not all species studied).

²Forest types are coded as follows: TrB, tropical broadleaf; TeB, temperate broadleaf; TeN, temperate needleleaf (conifer); BoN, boreal needleleaf (conifer); TrS, tropical savanna.

³1. Mau *et al.* (2018); 2. Coble & Cavaleri (2014); 3. Sack *et al.* (2006); 4. Chin & Sillett (2017); 5. Wyka *et al.* (2012); 6. Atherton *et al.* (2017); 7. Kenzo *et al.* (2015); 8. Kusi & Karsai (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.* (2012); 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 *et al.* (1997); 21. Fauset *et al.* (2018); 22. Niinemets *et al.* (1998); 23. Ishida *et al.* (1999); 24. Millen & Clendon (1979); 25. Smith & Carter (1988); 26. Hadley & Smith (1987); 28. Baltzer & Thomas (2005); 29. Coble *et al.* (2016); 30. Scartazza *et al.* (2016); 31. Duursma & Marshall (2006); 32. Harley *et al.* (1996); 33. Hernández *et al.* (2020); 34. Turnbull *et al.* (2003); 35. Chen *et al.* (2020); 36. van de Weg *et al.* (2012); 37. Cavaleri *et al.* (2008); 38. Königer *et al.* (1995); 39. Matsubara *et al.* (2009); 40. Harris & Medina (2013); 41. Hansen *et al.* (2002); 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 & Scoffoni (2013); 48. Ball *et al.* (1988); 49. Taylor *et al.* (2021); 50. Niinemets *et al.* (2010); 51. Brooks *et al.* (1997); 52. Curtis *et al.* (2019); 53. Slot *et al.* (2019); 54. Hamerlynck & Knapp (1996); 55. Lloyd *et al.* (2010); 56. Augspurger & Bartlett (2003); 57. Osada *et al.* (2001); 58. Meakem *et al.* (2018); 59. Condit *et al.* (2000); 60. Harley *et al.* (1997); 61. Niinemets & Sun (2015); 62. Sharkey & Monson (2014); 63. Šimpraga *et al.* (2013); 64. Domingues *et al.* (2005).

⁴Composite climatic stress variable integrating temperature, vapor pressure deficit, and relative humidity is higher in lower canopy.

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 (Laotawornkitkul *et al.*, 2009; Riedlmeier *et al.*, 2017; Lantz *et al.*, 2019; Monson *et al.*, 2021). Due to its much higher emission rate and relative ease of detectability, isoprene has received far more study in the field, although both isoprene and monoterpenes are expressed by many angiosperms and gymnosperms across all biomes (see Taylor *et al.*, 2021, and references therein).

Fewer than half of tree species express significant light-dependent isoprene emissions (Kesselmeier & Staudt, 1999; Taylor *et al.*, 2018), such that vertical variation in emissions is influenced by both vertical variation in species compositions and by plasticity in emission rate capacities (Taylor *et al.*, 2021). Within species, isoprene emission tends to increase toward brighter and hotter microenvironments (Niinemets, 2007), and across landscapes, emitting species are more abundant in 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 midcanopy of an Amazonian forest (Table 1; Taylor *et al.*, 2021). Similarly, within European beech crowns, monoterpene emissions were highest in

semishaded leaves beneath the canopy surface (Table 1; 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 midcanopy region (Section II.1; Sharkey *et al.*, 2008). Future work to understand how temporal dynamics of *T*_{leaf} vary with height 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 midcanopy thermal responses, while other traits play similar roles in upper canopy leaves.

Thermal tolerance Very high *T*_{leaf} (c. 40–60°C) irreversibly damages photosystem II, leading to leaf necrosis and death (Baker, 2008; Feeley *et al.*, 2020; Kunert *et al.*, 2022). Upper thermal thresholds for leaf survival can be imated by assessing the photosystem II functioning via using chlorophyll fluorescence techniques (Krause *et al.*, 2010). Thermal tolerance is described in terms of the *T*_{leaf}'s at which photosystem II efficiency starts to decrease (*T*_{crit}) and is reduced by 50%, *T*₅₀ (Slot *et al.*, 2021a). Thermal tolerances vary across species, being more closely linked to leaf traits than phylogeny (Feeley *et al.*, 2020; Slot *et al.*, 2021a),

and being greater in leaves that experience higher maximum temperatures (Perez & Feeley, 2020). 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 appear more closely adapted to microclimate than macroclimate (Feeley *et al.*, 2020; Slot *et al.*, 2021a).

Thermal tolerance is hypothesized to be greatest for the leaves with the greatest radiation loads and highest temperatures along the vertical gradient. Indeed, considering sun and shade leaf differences across the vertical profile of a closed-canopy forest in Panama, T_{50} was 0.7–1.4°C lower for shade than sun leaves for two of three tree species (Table 1; Slot *et al.*, 2019). Similarly, within a very open *Acacia papyrocarpa* canopy, T_{50} was highest (*albiet* by < 1°C) in the lower, north-facing leaves, which faced the greatest composite climate stress (low wind speed, greater radiation and T_{air} , and lower rates of heat dissipation) (Table 1; Curtis *et al.*, 2019). These modest differences in T_{50} coupled with larger differences in T_{leaf} across thermal microenvironments imply that more thermally tolerant sun leaves tend to operate closer to their thermal limits and could therefore be more vulnerable to heat anomalies (Perez & Feeley, 2020). However, not enough studies have evaluated thermal tolerances across vertical gradients to make robust inferences.

Leaf phenology Leaf phenology influences the vertical structure of microenvironments, T_{leaf} , and forest photosynthetic capacity (Rey-Sánchez *et al.*, 2016). In deciduous forests, the timing and extent of seasonal leaf gain and loss is structured across the vertical profile. In temperate climates, seasonal warming occurs earlier in the sheltered understory, facilitating earlier spring budbreak compared with the cooler upper canopy (Augspurger & Bartlett, 2003). Early leaf-out gives saplings and seedlings a window for high photosynthesis before they are shaded by canopy leaves – contributing the majority of annual carbon fixation for some seedlings – before canopy foliage and reduces light availability (Augspurger & Bartlett, 2003; Lee & Ibáñez, 2021). Within tropical dry-season-deciduous species, the fraction of seasonally deciduous individuals is greater in larger trees in hotter, brighter environments, with understory individuals typically remaining evergreen (Condit *et al.*, 2000). Similarly, fractions of deciduous species increase with tree size class (Condit *et al.*, 2000; Meakem *et al.*, 2018). Even in evergreen tropical forests, seasonal variation in leaf quantities follows distinct vertical patterns throughout the vertical profile depending on height and light environments (Tang & Dubayah, 2017; Smith *et al.*, 2019; Nunes *et al.*, 2022). For instance, in a central Amazonian forest, the upper canopies of both interior and edge forests shed leaves when maximum daily T_{air} exceeded *c.* 35°C (Nunes *et al.*, 2022). In evergreen forests, leaf turnover is faster in the upper canopy than in the understory (Osada *et al.*, 2001), and as a result, upper canopy leaves are, on average, younger than shade leaves. Leaf age distributions affect forest photosynthetic capacity (Niinemets, 2016; Wu *et al.*, 2016) and stress tolerance via age-specific leaf function (Kikuzawa & Lechowicz, 2006; Zhou *et al.*, 2015; Albert *et al.*, 2018). Leaf phenology thereby both responds to and influences the vertical structure of forest microenvironments and function.

4. Leaf gas exchange and its thermal sensitivity

Leaf gas exchange is strongly shaped by environmental drivers, T_{leaf} , and traits, all of which vary across vertical forest gradients (Sections II.1–II.3; Fig. 1). However, as we detail below, few studies have evaluated how temperature responses of leaf metabolic rates are shaped by the varying environmental conditions across vertical forest gradients (Table 2).

Conductance Leaf hydraulic, stomatal, and boundary layer conductances are all critical for regulating T_{leaf} via latent heat loss (Fig. 3). Due to higher wind, lower RH, and smaller leaf sizes in the upper canopy (Fig. 2; Table 1), g_b increases with height (Table 2). Maximum g_s increases with light – typically tracking photosynthetic capacity (Wong *et al.*, 1979) – and is thus higher in the sun-exposed upper canopy than in subcanopy or understory leaves (Table 2). However, water supply cannot meet the demands caused by the high radiation and g_b in sun leaves with fully open stomata, in part because of height-related constraints on water transport (Yoder *et al.*, 1994; Koch *et al.*, 2004; Sillett *et al.*, 2010) and/or increased leaf-air VPD caused by leaf warming in sunlit canopy locations (Buckley *et al.*, 2014). These constraints tend to reduce leaf water potential, making midday stomatal depression more prevalent in sun leaves than shade leaves in closed-canopy forests (Table 2), which drives the lower intracellular CO_2 and $\delta^{13}C$ (see Section II.3 subsection 'Metabolic capacity and efficiency'; Table 1). Stomatal depression reduces transpirational cooling (Fig. 3e), thus amplifying the warming of sun leaves by high radiation (Koch *et al.*, 1994; Zwieniecki *et al.*, 2004; Kosugi & Matsuo, 2006; Sanches *et al.*, 2010). The temperature at which g_s is greatest, 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} (driven by increased VPD) than lower canopy shade leaves (Hernández *et al.*, 2020; Carter *et al.*, 2021). Available data also suggest that high T_{air} can directly drive stomatal opening, if vapor pressure is experimentally adjusted in tandem with T_{air} to keep VPD constant (Fredeen & Sage, 1999; Mott & Peak, 2010; Urban *et al.*, 2017), although it appears that the negative effect of temperature on g_s , mediated by VPD, generally overrides the positive effect of temperature *per se* in nature, causing g_s to decline when the leaf warms.

Photosynthesis Photosynthetic capacity is generally higher in exposed canopy positions – a fact that is both predicted by optimization theory (Field, 1983; Hirose & Werger, 1987) and observed in numerous field studies (Table 2).

Temperature can affect photosynthesis directly, by altering photosynthetic enzyme activity and the electron transport chain, and indirectly, by increasing VPD and closing stomata (Lloyd & Farquhar, 2008). Photosynthesis has a peaked response to T_{air} , with the optimum commonly corresponding to the prevalent ambient growing season temperature (Doughty & Goulden, 2008; Slot & Winter, 2017; Tan *et al.*, 2017). Beyond the optimum, photosynthesis decreases due to stomatal closure (Slot & Winter, 2017; Grossiord *et al.*, 2020; Smith *et al.*, 2020) and biochemical

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.

Trait	Symbol	Units	Response ¹	Forest type(s) ²	Reference(s) ³
Conductance					
Boundary layer conductance	g_b	$\text{mmol m}^{-2} \text{ s}^{-1}$ mm s^{-1}	↑ H	TrB	3
			↑ H	TeN	12
			≈ L	TeN	12
Leaf hydraulic conductance	K_{leaf}	$\text{m}^{-2} \text{ s}^{-1} \text{ MPa}^{-1}$	↑ L	TeB	
Cuticle conductance	g_{min}	$\text{mmol m}^{-2} \text{ s}^{-1}$	↑ L	TrB	38
Max stomatal conductance	$g_{s \text{ max}}$	$\text{mol m}^{-2} \text{ s}^{-1}$	↑ 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, 39, 5, 6, 7
			↑ L	TrB, TeN	9, 39, 7, 27
Stomatal conductance at optimal temperature	$g_s \text{ at } T_{\text{opt}}$	$\text{mol m}^{-2} \text{ s}^{-1}$	≈ ↑ H	TeB	11
			↓ H	TrB	39
			≈ ↑ 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, 2
Maximum light-saturated net photosynthesis	A_{sat}	$\mu\text{mol m}^{-2} \text{ s}^{-1}$	≈ L	TrB, TeB, TeN	20, 19
			↑ H	TrB, TeB	21, 22
A_{sat} at optimum temperature	A_{opt}	$\mu\text{mol m}^{-2} \text{ s}^{-1}$	↑ L	TrB, TeB	8, 22
			≈ ↑ H	TrB, TeB	13, 11
			↑ H	TrB	39
Optimum temperature for photosynthesis	T_{opt}	°C	↑ L	TrB	8, 13
			≈ H	TrB, TeB	23, 11, 13
			↓ H	TrB	39
Photosynthetic light compensation point	LCP	$\mu\text{mol m}^{-2}$	≈ L	TrB, TeB	9, 8, 11
			↑ H	TrB, TeB, TeN	24, 16
Maximal carboxylation rate	V_{cmax}	$\mu\text{mol m}^{-2} \text{ s}^{-1}$	↑ L	TrB, TeB, TeN	8, 17, 16
			↑ H	TrB, TeB	2, 39, 22, 14
			↑ L	TrB, TeB, BoN	9, 39, 22, 14, 10
			≈ H	TrB, TeB	2, 2
Optimum temperature for V_{cmax}	$V_{\text{cmax}} (T_{\text{opt}})$	$\text{nmol g}^{-1} \text{ s}^{-1}$	≈ L	TrB, TeB	2, 22
			≈ ↓ L	TeB	25
			≈ ↑ H	TeB	11
			≈ L	TrB	9
Electron transport rate	J_{max}	$\mu\text{mol m}^{-2} \text{ s}^{-1}$	≈ H	TrB, TeB	2, 39, 36, 22, 14
			↑ L	TrB, TeB	9, 39, 22, 26, 14
			≈ H	TrB, TeB	2, 22
			≈ L	TrB, TeB	2, 22
Optimal temperature of J_{max}	T_{optETR} $J_{\text{max}} (T_{\text{opt}})$	$\text{nmol e}^{-1} \text{ g}^{-1} \text{ s}^{-1}$ °C	≈ ↓ L	TeB	25
			↓ H	TrB	39
			≈ L	TrB	9
High-temperature CO ₂ compensation point	T_{max}	°C	≈ H	TrB	21
			≈ L	TrB	8
Respiration					
Respiration rate at 25°C	R	$\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ $\mu\text{mol CO}_2 \text{ kg}^{-1} \text{ s}^{-1}$	↑ H	TrB, TeB, TeN	36, 28, 29, 30
			≈ H	TrB, TeB, TeN	28, 29
			↑ L	TrB, TeN	28, 30
Light respiration	R_L	$\mu\text{mol m}^{-2} \text{ s}^{-1}$	↑ H	TrB	21
			↑ L	TrB	21
Dark respiration	R_{dark}	$\mu\text{mol m}^{-2} \text{ s}^{-1}$	↑ H	TrB, TeB, BoN	21, 14, 31, 22, 38
			↑ L	TrB, TeB, TeN, BoN	21, 14, 22, 17, 10, 35
			≈ ↑ H	TrB	2, 32
R_{dark} at reference T	R_{dark} at reference T	$\mu\text{mol m}^{-2} \text{ s}^{-1}$ $\mu\text{mol (kg leaf)}^{-1} \text{ s}^{-1}$ $\mu\text{mol (kg N)}^{-1} \text{ s}^{-1}$ $\mu\text{mol m}^{-2} \text{ s}^{-1}$	≈ L	TrB	2, 32
			↑ H	TrB, TeB, TeN	21, 14, 31, 29
			↑ H	TrB, TeB, TeN	21, 14, 31, 21
			↑ H	TeB, TeN	3, 29
			↑ L	TrB, TeB	2, 8, 34

Table 2 (Continued)

Trait	Symbol	Units	Response ¹	Forest type(s) ²	Reference(s) ³
Temperature sensitivity of R_{dark}	Q_{10}	$^{\circ}\text{C}^{-1}$ $^{\circ}\text{C}^{-1}$	$\approx \text{H}$	TrB, TeB, TeN	21, 36, 31, 30
			$\approx \uparrow \text{H}$	TeB, TeN	3, 29
			$\approx \downarrow \text{L}$	TrB, TeB, TeN	21, 31, 30
			$\uparrow \text{L}$	TeB	33
Activation energy of R_{dark}	E_0	$\text{kJ mol}^{-1} \text{K}^{-1}$	$\approx \text{H}$	TrB, TeB, TeN	21, 34, 29
			$\approx \text{L}$	TrB	21, 8

Studies listed here were compiled using a systematic review process, as described in Supporting Information Methods S3.

¹Responses 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 nonsignificant or mixed trends (e.g. significant in some but not all species studied).

²Forest types are coded as follows: TrB, tropical broadleaf; TeB, temperate broadleaf; TeN, temperate needleleaf (conifer); BoN, boreal needleleaf (conifer).

³1. 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.* (2010); 7. Zweifel *et al.* (2002); 8. Slot *et al.* (2019); 9. Hernández *et al.* (2020); 10. Urban *et al.* (2007); 11. Carter & Cavaleri (2018); 12. Martin *et al.* (1999); 13. Mau *et al.* (2018); 14. Kosugi *et al.* (2012); 15. Niinemets *et al.* (2015a,b); 16. Bachofen *et al.* (2020); 17. Hamerlynck & Knapp (1996); 18. Coble *et al.* (2016); 19. Wyka *et al.* (2012); 20. Rijkers *et al.* (2000); 21. Weerasinghe *et al.* (2014); 22. Scartazza *et al.* (2016); 23. Miller *et al.* (2021); 24. Harris & Medina (2013); 25. Legner *et al.* (2014); 26. Kitao *et al.* (2012); 27. Fauset *et al.* (2018); 28. Meir *et al.* (2001); 29. Turnbull *et al.* (2003); 30. Araki *et al.* (2017); 31. Bolstad *et al.* (1999); 32. Kenzo *et al.* (2015); 33. Harley *et al.* (1996); 34. Xu & Griffin (2006); 35. Atherton *et al.* (2017); 36. Carter *et al.* (2021); 37. Sack *et al.* (2003); 38. Slot *et al.* (2021b); 39. Carswell *et al.* (2000).

constraints (Sharkey, 2005; Vårhammar *et al.*, 2015; Kumarathunge *et al.*, 2019).

We have very little evidence about how the temperature sensitivity of photosynthesis compares between sun and shade leaves, and existing studies, which compare sun and shade leaves of the same trees, reveal no pronounced overall trend with height in photosynthetic temperature optima (Table 2). Based on consistent positive relationships between growth temperature and optimum temperature of photosynthesis (T_{opt}) across sites and seasons (Tan *et al.*, 2017; Kumarathunge *et al.*, 2019), one might expect sun leaves to have a stronger temperature dependence and higher T_{opt} 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, 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_{max}) and regeneration rates (J_{max}) did not differ systematically between tropical sun and shade leaves (Hernández *et al.*, 2020), nor within-canopies of tropical and temperate trees (Mau *et al.*, 2018; Miller *et al.*, 2021). By contrast, tropical experimental warming observations showed that T_{opt} and T_{opt} of J_{max} decrease from the understory to the top of the canopy, potentially linked to greater thermal sensitivity of g_s in upper canopy leaves (Carter *et al.*, 2021). The observed lack of sun–shade differences in T_{opt} may reflect acclimation to similar temperatures of peak photosynthesis (Hernández *et al.*, 2020). 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 forest vertical profile. In the meantime, it remains unresolved whether photosynthesis is more affected by

high temperatures in upper canopy or understory leaves, and how this might vary across forest types and environmental conditions.

Respiration Similar to photosynthesis, respiration tends to be higher in upper canopy sun leaves, but its temperature sensitivity (Q_{10} or E_0) shows no definite trend along the vertical gradient. Specifically, the temperature sensitivity of respiration can be constant within vertical profiles and in seedling sun vs shade leaves, greater in upper canopy leaves, or greater in the lower canopy (Table 2). 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} (Slot & Kitajima, 2015; Carter *et al.*, 2021). Overall, although the temperature difference between upper and lower canopy positions is an important driver of respiration, we currently lack mechanistic understanding of how and why its temperature sensitivity varies across the forest vertical profile.

5. Tree and ecosystem ecology

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

Tree metabolism, growth, and survival Tree metabolism and growth are shaped by crown location in the vertical gradient. Tree height, crown volume, and foliage biomass all scale with diameter at breast height (DBH), which strongly predicts tree transpiration (Meinzer *et al.*, 2001; Anderson-Teixeira *et al.*, 2015; Kunert *et al.*, 2017) photosynthesis, and intracanopy trait variation (Bin *et al.*, 2022). Specifically, increases are linked to greater leaf area and the increasing probability that the crown is in the canopy (Muller-Landau *et al.*, 2006), where leaves receive more light and have higher leaf area-specific photosynthesis (Table 2). Photosynthate

production is allocated among functions including respiration, aboveground woody growth, foliar turnover, root growth and allocation to root-associated microorganisms, reproduction, defense, and storage of nonstructural carbohydrates (NSCs). Among these, the best-studied process is aboveground woody growth, which consumes only a modest fraction of total photosynthate (*c.* 1/6 on the ecosystem level; Anderson-Teixeira *et al.*, 2021), but is critically important to long-term forest dynamics and carbon cycling because woody tissues have 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.*, 2022). In open forests and for open-growth individual trees, growth rate declines with DBH, 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, 2022). This points to a dominant role of vertical profiles in the biophysical environment, particularly light, in shaping tree growth rates within forests.

Vertical gradients also affect the climate sensitivity of metabolism and growth. Stomatal conductance can be strongly limited by high VPD even when soil water is plentiful (Corlett, 2011; Novick *et al.*, 2016; Ruehr *et al.*, 2016). Therefore, periods of high VPD, whether on timescales of hours, days, or seasons, tend to reduce transpiration and photosynthesis more in tall trees that occupy canopy positions in closed-canopy forests (Christoffersen *et al.*, 2016; Garcia *et al.*, 2021). This is consistent with observations that both dry season leaf loss (see Section II.3 subsection 'Leaf phenology'; Table 1) and g_s limitation (see Section II.4 subsection 'Conductance'; Table 2) increase with height across the vertical profile. More active regulation of transpiration by tall canopy trees (Mediavilla & Escudero, 2004) – often combined with greater effective rooting depth – may offset greater xylem embolism risk (Olson *et al.*, 2018; Chitra-Tarak *et al.*, 2021; Garcia *et al.*, 2021) and reduce the need to adjust carbon metabolism traits during drought (Bartholomew *et al.*, 2020). This reduces carbon isotope discrimination, indicative of greater g_s limitation, with increasing tree height (Table 1; McDowell *et al.*, 2011).

In turn, the drought sensitivity of woody growth tends to be greater in upper canopy trees than in smaller trees with less exposed crowns. Dendrochronologists generally agree that tree ring records of large, exposed trees are best suited for climate reconstructions because their annual growth is most sensitive to interannual climate variation (Fritts, 1976). However, few studies have directly examined drought- or temperature sensitivities as a function of tree size. Most have found greater sensitivity to low precipitation or seasonally high temperatures among larger, more exposed trees (Fig. 4; Trouillier *et al.*, 2018; Gillerot *et al.*, 2020; McGregor *et al.*, 2021; Anderson-Teixeira *et al.*, 2022; Heilman *et al.*, 2022), corroborating evidence from global forest censuses that drought reduces growth more in large trees (Bennett *et al.*, 2015). Drought also causes greater mortality in larger trees (Bennett *et al.*, 2015; Stovall *et al.*, 2019). Mechanistically, this is likely driven in part by larger trees having their crowns in microenvironments that are more challenging during drought (Figs 1–3; Scharnweber *et al.*, 2019), yet height itself also creates 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 and closed-canopy forests (Bennett *et al.*, 2015; Anderson-Teixeira *et al.*, 2022). However, evidence that short trees in young stands can be more drought-sensitive than taller trees in mature forests (Irvine *et al.*, 2004; Wang *et al.*, 2022) reinforces the importance of exposure in shaping drought sensitivity. The relative importance of exposure vs height in shaping drought sensitivity remains to be disentangled.

Although drought sensitivity clearly increases with crown height and hence with DBH, it remains unclear how growth sensitivity to high T_{air} , independent of drought, varies along the vertical gradient. High T_{air} is often associated with high VPD and atmospheric drought, likely explaining negative growth responses to T_{air} – 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.*, 2022). However, under well-watered conditions conducive to high g_s , we do not necessarily expect higher thermal sensitivity of photosynthesis (see Section II.4 subsection 'Photosynthesis') or woody growth in upper canopy trees than their understory counterparts. Indeed, there are cases where tree ring records show more negative or less positive T_{air} -responses of understory trees than canopy dominants (Rollinson *et al.*, 2020; Anderson-Teixeira *et al.*, 2022). Additional research is required to understand the mechanisms underlying these intriguing differences, and to disentangle size-related tree growth responses to hot-wet vs hot-dry conditions.

Carbon 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 evapotranspiration (ET) and transpiration have been shown to increase with height in a *Picea abies* forest in Germany, where 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 *c.* 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 carbon cycling, it has been estimated that the canopy strata contribute $\geq 64\%$ of net daytime CO_2 uptake (i.e. gross primary productivity (GPP) – ecosystem respiration, including from soil; Misson *et al.*, 2007). Large trees also dominate woody aboveground net primary productivity ($ANPP_{woody}$) and mortality (M_{woody}), with trees ≥ 10 cm DBH usually contributing > 85% of $ANPP_{woody}$ and M_{woody} across 25 globally distributed forests (Fig. 5b; Piconiot *et al.*, 2022).

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 under conditions of moderate-to-high VPD, transpiration, GPP, and $ANPP_{woody}$ should all be more sensitive to high temperatures in the upper canopy than in the understory (Grossiord *et al.*, 2020; Nunes *et al.*, 2022). Because canopy trees dominate these fluxes (Fig. 5), their responses will strongly influence the whole-ecosystem response, potentially with modest buffering by the understory.

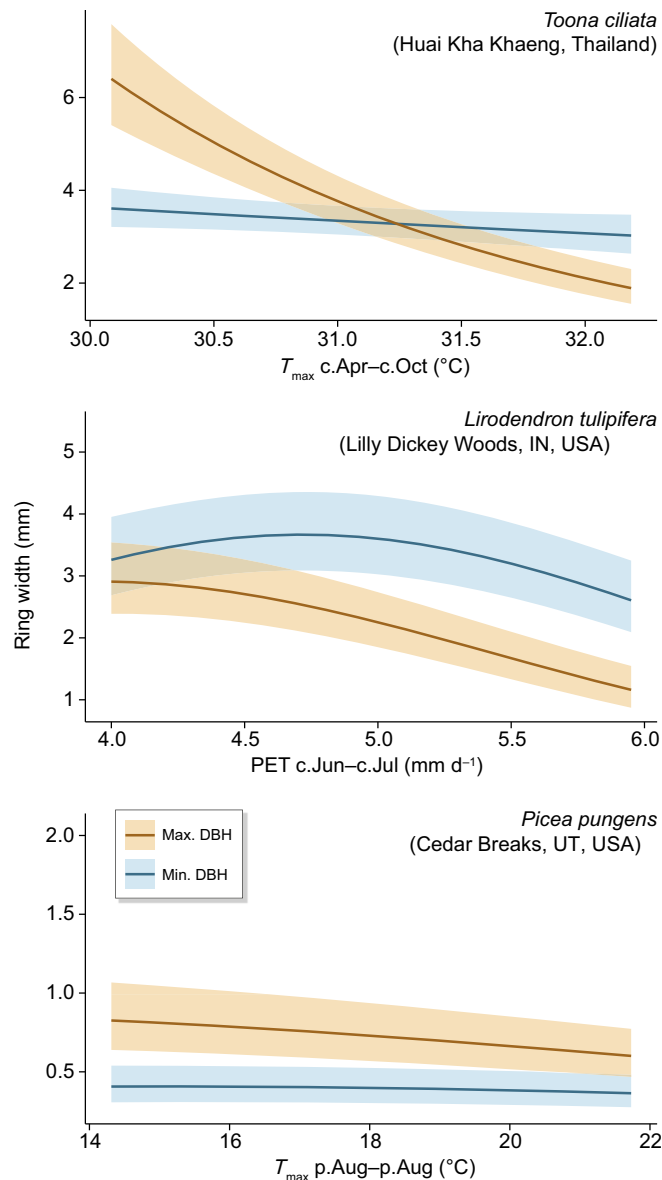


Fig. 4 Examples of tree ring evidence for greater interannual temperature sensitivity of annual growth for large than for small trees. Across three sites and species, trees with large diameter at breast height (DBH) had more negative growth responses to high maximum temperature (T_{\max}) or potential evapotranspiration (PET) than did small trees of the same species. Independent variables are the most influential temperature-related variable at the site (T_{\max} or PET over a seasonal window spanning from the noted beginning to end month, where 'c' and 'p' represent months in the current and previous calendar year, respectively). Colored lines represent responses of trees at the maximum and minimum tails of the DBH distribution included in the analysis 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. Redrawn from Anderson-Teixeira *et al.* (2022).

Thus, for example, increases in canopy temperature reduce forest GPP in the tropics (Pau *et al.*, 2018). Yet, evidence also suggests 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; Nunes *et al.*, 2022). A rare example of a study comparing 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 trees 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 some tree ring evidence (Rollinson *et al.*, 2020; Anderson-Teixeira *et al.*, 2022) raise the possibility that understory trees may be at a relative disadvantage under hot, humid 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 to the implications of these patterns for understanding how forest ecosystems may be impacted by global change, and our ability to project this across space and time.

1. Global change responses

The complex interwoven relations between the biophysical environment and biological factors – leaf traits, metabolic processes, and distribution of species across forest 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 in nighttime T_{air} , as well as increased maximum temperatures, with extreme increases during heat waves (IPCC, 2021). To the extent that warming is coupled with drought, we expect that tall trees with exposed crowns will usually be hardest-hit, particularly in severe drought, partly because their crowns are positioned in a more challenging microenvironment (see Section II.5 subsection ‘Tree metabolism, growth, and survival’; Figs 1–4). By 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; Hogan *et al.*, 2019; Nunes *et al.*, 2022). It remains unclear how these patterns vary with the nature of the drought, including the relative contributions to stress from low soil moisture vs high VPD. While the two are coupled over longer timescales (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 high VPD in particular skews the stress more toward the exposed canopy trees.

It remains uncertain how responses to warming will vary across vertical gradients under mesic conditions. Leaves display substantial plasticity to adapt to warmer temperatures (Cunningham & Read, 2003; Way, 2019; Slot *et al.*, 2021c) and to recover from heat stress (Smith *et al.*, 2020), yet failure to fully acclimate will reduce carbon sequestration at leaf, tree, and ecosystem levels (Tan

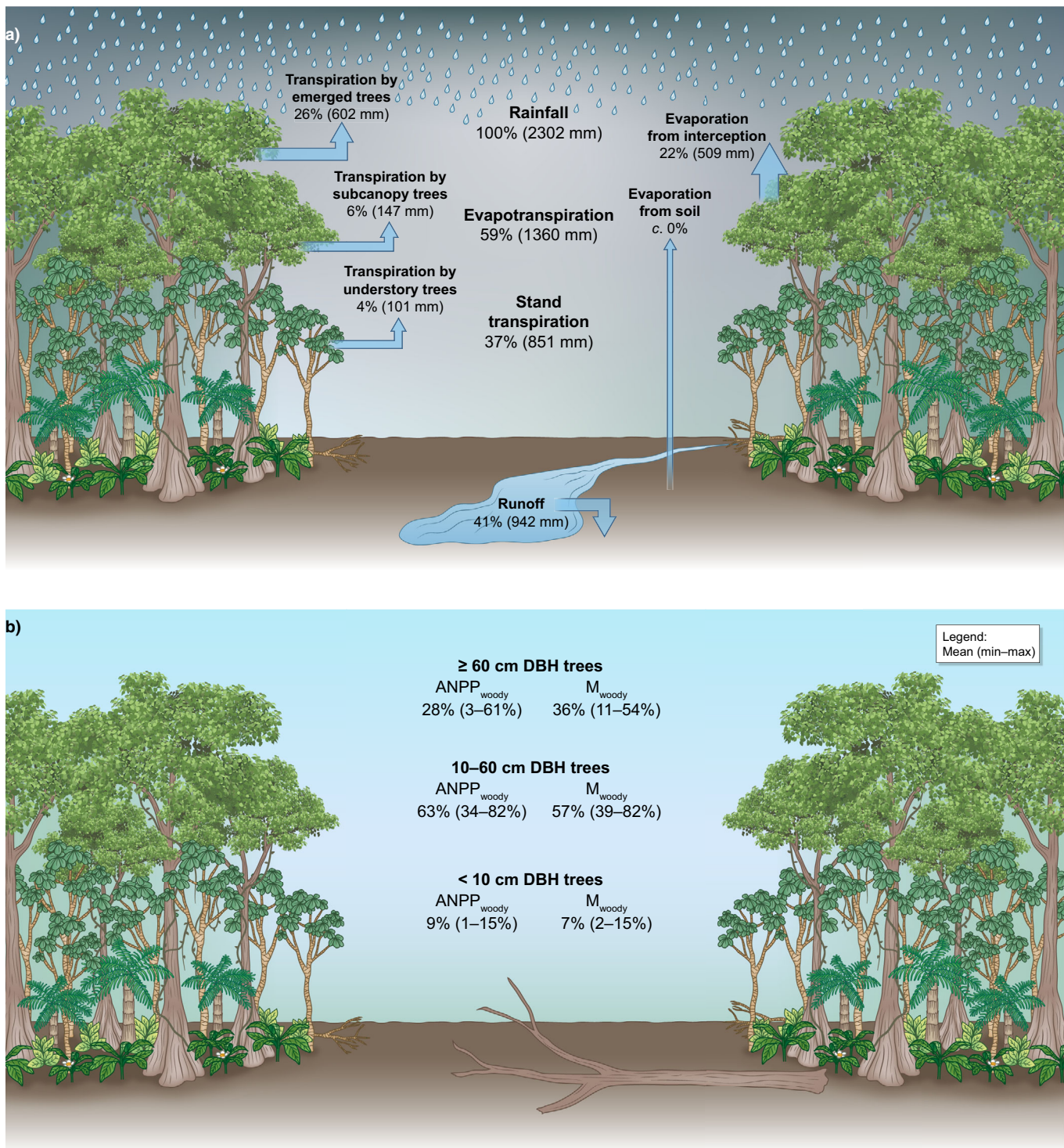


Fig. 5 Vertical partitioning of (a) evapotranspiration and (b) carbon fluxes in tropical forests. Panel (a) is from Kunert *et al.* (2017); (b) presents averages for 14 tropical forests from Pioniot *et al.* (2022). DBH, diameter at breast height; ANPP, aboveground net primary productivity; M_{woody} , woody mortality.

et al., 2017; Huang *et al.*, 2019; Way, 2019; Bennett *et al.*, 2021). As growing season T_{air} increasingly equals or exceeds photosynthetic optima (Slot & Winter, 2017; Mau *et al.*, 2018; Huang *et al.*, 2019; Kumarathunge *et al.*, 2019), exposed crowns are likely to be most vulnerable. Particularly in midlatitude forests, which have the narrowest thermal safety margin between historical

maximum temperatures and T_{crit} (O'Sullivan *et al.*, 2017), T_{leaf} of sun-exposed leaves may approach tolerance thresholds during heat waves, causing photosynthetic decline or even leaf death (O'Sullivan *et al.*, 2017; Tiwari *et al.*, 2021; Kunert *et al.*, 2022). By contrast, understory leaves and trees are unlikely to face the same absolute extremes of T_{leaf} , and protection from thermal stress

associated with high direct radiation 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 dissipate excess heat may prove disadvantageous. While it is currently difficult to predict whether canopy or understory photosynthesis will be more severely affected by warming (see Section II.4 subsection 'Photosynthesis'), limited tree ring evidence indicates that unusually hot growing seasons can dramatically reduce the growth of understory trees (Rollinson *et al.*, 2020), and these small trees may be at higher risk of carbon starvation because they have lower NSC reserves (Niinemets, 2010). Thus, despite their buffered microclimate, it is possible that understory trees could be more adversely impacted by warming temperatures than their canopy counterparts under some conditions.

Canopy disturbance Increasing severity and frequency of heat waves, accompanied with increases in VPD and ET, places canopy trees at particularly elevated risk of mortality (see Section II.5 subsection 'Tree metabolism, growth, and survival'), potentially causing large-scale canopy dieback (Matusick *et al.*, 2013; Teskey *et al.*, 2015; Breshears *et al.*, 2021). Large trees are also the most vulnerable to other climate-related disturbances (e.g. wind and lightning; Gora & Esquivel-Muelbert, 2021) that are expected to intensify with climate change (IPCC, 2021), and they are also targeted by selective logging (Miller *et al.*, 2011). Forest fragmentation also 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 radiation and temperatures within the forest (Jucker *et al.*, 2018; Stark *et al.*, 2020). Such changes often enhance growth of smaller trees, which benefit from increased light (Bennett *et al.*, 2015; Hogan *et al.*, 2019; Nunes *et al.*, 2022), and wetter forests can prove quite resilient to canopy disturbance (Miller *et al.*, 2011). However, this shift to hotter and drier microclimates makes some forests more susceptible to further disturbances, for example, increasing fire risk (Brando *et al.*, 2014; Aragão *et al.*, 2018). Severe degradation can cause dramatic ecological state changes (e.g. the transition of tropical forests to more open, savanna-like vegetation) and nonlinear 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, 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 may not recover and persist after severe canopy disturbance (Flores *et al.*, 2017; Tepley *et al.*, 2017; Miller *et al.*, 2019; McDowell *et al.*, 2020).

Canopy disturbance poses an increasing threat to the biodiversity of understory species that are otherwise buffered from climatic extremes (Scheffers *et al.*, 2013; Greiser *et al.*, 2019). Canopy structure affects understory species composition, which has been shown to shift under warming and canopy disturbance (Bertrand *et al.*, 2020; Maes *et al.*, 2020; Majasalmi & Rautiainen, 2020). In the understory, warming reduces the abundance of less thermally

adapted plant species, causing thermophilization of the plant community (Duque *et al.*, 2015; Greiser *et al.*, 2019; Zellweger *et al.*, 2020). If compositional shifts toward more thermally adapted species fail to keep pace with warming, the ecosystem-level resilience to canopy disturbance that is often provided by smaller trees (Miller *et al.*, 2011) will be destroyed, resulting in breakdown of canopy structure and the potential state changes described above.

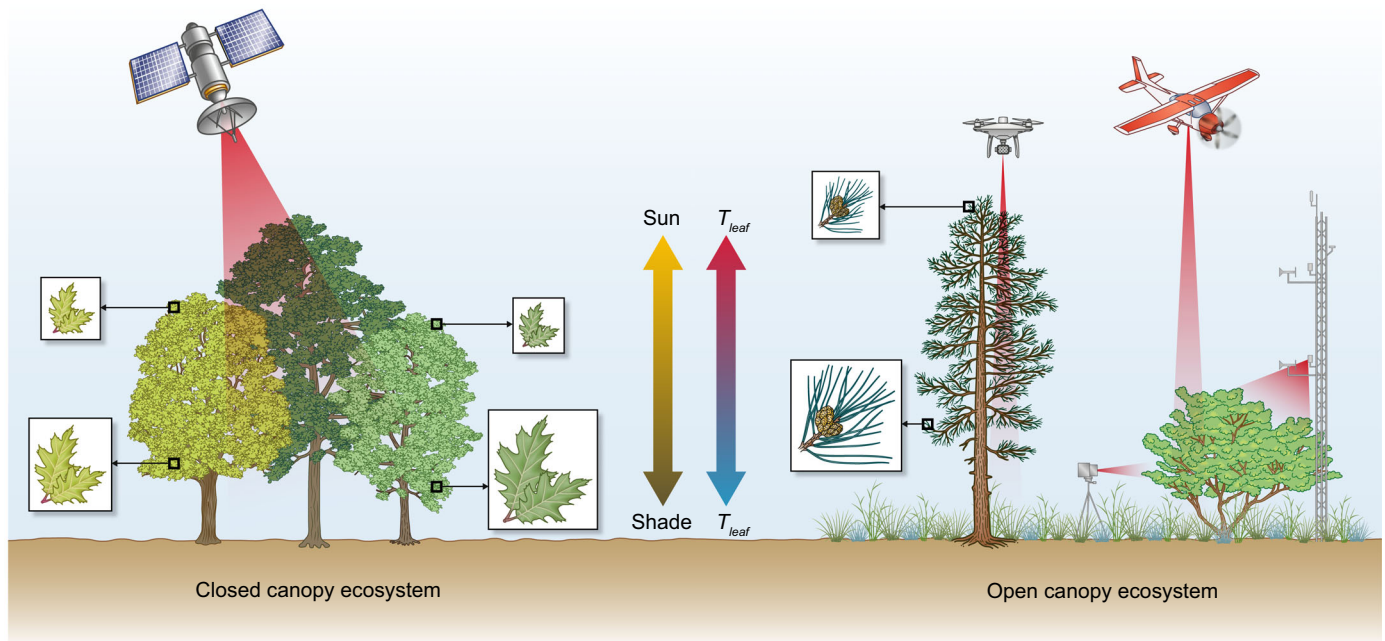
2. Scaling across space and time

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 feedback between the world's forests and climate change, these mechanisms must be sufficiently represented in models and scaled spatially via remote sensing.

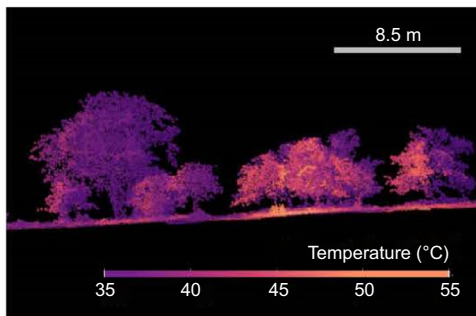
Representing vertical gradients in models Dynamic global vegetation models (DGVMs), which comprise the land surface models in Earth system models, are used to predict the global distribution of vegetation types and biosphere–atmosphere feedback (Foley *et al.*, 1996; Sitch *et al.*, 2003; Woodward & Lomas, 2004). Dynamic global vegetation models 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 light environment and microclimates at high 3D spatial resolution (Shugart *et al.*, 2018), to big-leaf models that reduce 3D vegetation structure to single vegetation layer, implicitly capturing vertical profiles in light, photosynthetic capacity and other features by assuming those profiles are exponential and thus can be integrated analytically (Bonan *et al.*, 2003; Krinner *et al.*, 2005). This simplification is computationally more efficient but does not always capture observed vertical profiles (Sections II.1–II.4; for example, vertical shifts in the balance between stomatal conductance and photosynthetic capacity, see Section II.4 subsections 'Conductance' and 'Photosynthesis') and cannot capture important demographic processes and vertical light competition (Hurt *et al.*, 1998; Smith *et al.*, 2001; Krinner *et al.*, 2005). The computational middle-ground lies in cohort-based models, which represent vegetation as cohorts of individuals, grouped together based on properties, including size, age, and functional type (Fisher *et al.*, 2018).

Owing to differences in the representation of forest vertical strata, DGVMs vary in their capacity to incorporate vertical variation in leaf traits and physiological processes. In general, however, this variation is accounted for via light competition. Models partition radiation above and within the forest vertical profile (i.e. direct vs diffuse light) using radiative transfer models or a system of two coupled ordinary differential equations, referred to as a two-stream imation (Sellers, 1985; Fisher *et al.*, 2018). Using the latter method, single canopy layers are divided into sun and shade fractions (e.g. in the Community Land Model), while models with multiple vegetative layers can analytically solve the two-stream imation for each layer. Thus, even in single-layer models, key physiological parameters such as V_{cmax} and J_{max} vary, decreasing with increasing cumulative LAI or lower light conditions (Table 2;

(a) Integrating vertically resolved *in situ* data with lidar and thermal infrared remote sensing data



(b) Remote sensing data



(c) Ecosystem modeling

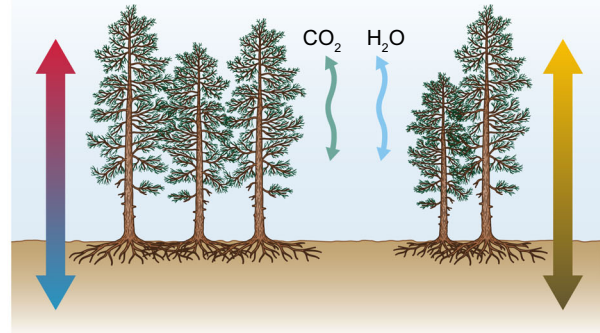


Fig. 6 LiDAR and thermal remote sensing data can be used to measure vertical forest structure and plant thermal signatures at increasingly large scales. (a, b) Integrating *in situ* and remote sensing measurements will support our ability to scale understanding of vertical gradients within and across 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 Tables 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. T_{leaf} , leaf temperature.

Krinner *et al.*, 2005). Recent years have seen growing efforts to incorporate vertical variation more directly in models, specifically involving leaf water potential and light absorption, along with an increasing interest in confronting models directly with field measurements (Fisher & Koven, 2020; Maclean & Klimes, 2021). Recent model developments at the cutting edge of representing vertical variation (Bonan *et al.*, 2018; Chen *et al.*, 2019; Longo *et al.*, 2019) implement vertical gradients of irradiance, water content, T_{leaf} and humidification of canopy air by transpiration, modulated by turbulence within the forest and a roughness layer that extends to roughly twice the canopy height (Fisher & Koven, 2020).

The findings of this review reinforce the notion that representing vertical structuring is essential to capturing forest dynamics under

global change. Improved representation of vertical variation in forest structure and ecosystem function is critical for representing thermal sensitivity and has repeatedly been identified as important for reducing uncertainty and accurately characterizing biologically mediated feedback (Moorcroft *et al.*, 2001; Banerjee & Linn, 2018; Bonan *et al.*, 2021). Moreover, given the anticipated importance of midcanopy and understory trees in ecosystem resilience and given the increasing mortality of canopy trees, it is essential that models separately represent these strata. A key question is whether existing models adequately represent the processes that underpin understory and large tree responses to thermal stress. Most models have been developed to capture dynamics in the upper canopy, given the disproportionate role of large trees in ecosystem dynamics (Fig. 5). Less attention has focused on developing and validating understory

tree dynamics and responses to perturbations in models, in large part to the paucity of observational and experimental studies needed to resolve key patterns and underlying mechanisms (Sections II.4, II.5). Pairing of models with observational studies is key to further improving our mechanistic understanding of vertical gradients and their implications.

Although an improvement over big-leaf models, DGVMs that separate the canopy into only two layers (e.g. sunlit and shaded portions; De Pury & Farquhar, 1997) may not be able to capture important within-canopy variation in terms of leaf dynamics (e.g. seasonal shifts in vertical leaf area distributions; Table 1; Smith *et al.*, 2019) and functions (e.g. thermal responses; Table 2). Multilayered ecosystem models will likely be necessary for accurately predicting future forest function (Bonan *et al.*, 2021). In addition, capturing vertical gradients in ET, GPP, respiration, and woody growth, and subsequently the net ecosystem effects, requires improved characterization of the functional response of leaf-level processes to vertically varying abiotic conditions, and the role of traits 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 offers a promising opportunity for mapping vertical thermal gradients and vegetation structure across scales (Fig. 6). Airborne, spaceborne, and terrestrial laser scanning data yield detailed 3D reconstructions of whole tree and forest structure. These data can be combined with thermal remote sensing data from the spaceborne ECOSTRESS sensor (Hulley *et al.*, 2019; Fisher *et al.*, 2020) or drone- and tower-based infrared cameras.

Detailed structural information from LiDAR data can be 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). Canopy shading 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 (Davis *et al.*, 2019). Satellite and airborne thermal infrared remote sensing analyses are now being conducted at regional and continental scales, although few applications exist at finer scales needed to understand vertical variation in canopy temperatures (Johnston *et al.*, 2022). As an example of the type of insight possible with this approach, Pau *et al.* (2018) used the data from a tower-based infrared camera in combination with eddy-covariance data and found that tropical forest GPP was more strongly associated with canopy temperature than T_{air} or VPD. In a savanna system in the Western USA, Johnston *et al.* (2022) found lower foliage temperatures at the tops of tree crowns than in the understory, which was influenced by very high grass temperatures, consistent with the principles outlined in Sections II.1 and II.2 (Fig. S1). The growing availability of such data makes this an opportune time to link *in situ* measurements with fine- and landscape-scale

measurements 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, uncertainty remains about how temperature sensitivity of foliar gas exchange varies across these vertical gradients. Similarly, much remains unknown about how crown exposure influences the temperature sensitivity of woody stem growth. While most available data suggest that large canopy trees are the most vulnerable to warming when water is limited, far less is known about the responses of understory trees.

As climate changes, patterns and processes across vertical gradients will likely shift as well. In the historical climates to which trees adapted, the canopy was an advantageous place for photosynthesis and growth. However, as temperatures increase, it is likely that exposed canopy positions will become increasingly physiologically stressful. Ensuing increased mortality of canopy trees will create ever more gaps, changing understory conditions and community composition. Ultimately, mid- and understory tree communities will be critical to the resilience of forest ecosystems under changing climate, making improved understanding and model representation of their dynamics essential 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 crucial to understanding and forecasting forest–climate feedback in the coming decades.

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Author contributions

NV and KJA-T planned and designed the research, with contributions from all authors. NV reviewed the literature. NV, IRM, EMO and MNS contributed data and analyses. MS, TCT, LS and TNB contributed to writing and revising of the manuscript.

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Data availability

No new data were created in this study. New analyses are based on the data available from the National Ecological Observatory Network (NEON; <https://www.neonscience.org/>). The R scripts used for new analyses are available via GitHub (<https://github.com/EcoClimLab/vertical-thermal-review>) and archived in Zenodo (doi: [10.5281/zenodo.7050582](https://doi.org/10.5281/zenodo.7050582)).

References

- Abrams MD, Kubiske ME. 1990. Leaf structural characteristics of 31 hardwood and conifer tree species in central Wisconsin: influence of light regime and shade-tolerance rank. *Forest Ecology and Management* 31: 245–253.
- Albert LP, Wu J, Prohaska N, de Camargo PB, Huxman TE, Tribuzy ES, Ivanov VY, Oliveira RS, Garcia S, Smith MN *et al.* 2018. Age-dependent leaf physiology and consequences for crown-scale carbon uptake during the dry season in an Amazon evergreen forest. *New Phytologist* 219: 870–884.
- de Almeida DRA, Nelson BW, Schietti J, Gorgens EB, Resende AF, Stark SC, Valbuena R. 2016. Contrasting fire damage and fire susceptibility between seasonally flooded forest and upland forest in the central Amazon using portable profiling LiDAR. *Remote Sensing of Environment* 184: 153–160.
- Ambrose AR, Sillett SC, Koch GW, Van Pelt R, Antoine ME, Dawson TE. 2010. Effects of height on treecrop transpiration and stomatal conductance in coast redwood (*Sequoia sempervirens*). *Tree Physiology* 30: 1260–1272.
- Anderson-Teixeira KJ, Herrmann V, Banbury Morgan R, Bond-Lamberty B, Cook-Patton SC, Ferson AE, Muller-Landau HC, Wang MMH. 2021. Carbon cycling in mature and regrowth forests globally. *Environmental Research Letters* 16: 053009.
- Anderson-Teixeira KJ, Herrmann V, Rollinson CR, Gonzalez B, Gonzalez-Akre EB, Pederson N, Alexander MR, Allen CD, Alfaro-Sánchez R, Awada T *et al.* 2022. Joint effects of climate, tree size, and year on annual tree growth derived from tree-ring records of ten globally distributed forests. *Global Change Biology* 28: 245–266.
- Anderson-Teixeira KJ, McCarvey JC, Muller-Landau HC, Park JY, Gonzalez-Akre EB, Herrmann V, Bennett AC, So CV, Bourg NA, Thompson JR *et al.* 2015. Size-related scaling of tree form and function in a mixed-age forest. *Functional Ecology* 29: 1587–1602.
- Aragão LEOC, Anderson LO, Fonseca MG, Rosan TM, Vedovato LB, Wagner FH, Silva CVJ, Silva Junior CHL, Arai E, Aguiar AP *et al.* 2018. 21st Century drought-related fires counteract the decline of Amazon deforestation carbon emissions. *Nature Communications* 9: 536.
- Araki MG, Gyokusen K, Kajimoto T. 2017. Vertical and seasonal variations in temperature responses of leaf respiration in a *Chamaecyparis obtusa* canopy. *Tree Physiology* 37: 1269–1284.
- Arora VK, Katavouta A, Williams RG, Jones CD, Brovkin V, Friedlingstein P, Schwinger J, Bopp L, Boucher O, Cadule P *et al.* 2020. Carbon–concentration and carbon–climate feedbacks in CMIP6 models and their comparison to CMIP5 models. *Biogeosciences* 17: 4173–4222.
- von Arx G, Dobbervin M, Rebetez M. 2012. Spatio-temporal effects of forest canopy on understory microclimate in a long-term experiment in Switzerland. *Agricultural and Forest Meteorology* 166–167: 144–155.
- Ashton PS, Hall P. 1992. Comparisons of structure among mixed dipterocarp forests of north-western Borneo. *Journal of Ecology* 80: 459–481.
- Atherton J, Olascoaga B, Alonso L, Porcar-Castell A. 2017. Spatial variation of leaf optical properties in a boreal forest is influenced by species and light environment. *Frontiers in Plant Science* 8: 1–14.
- Augsburger CK, Bartlett EA. 2003. Differences in leaf phenology between juvenile and adult trees in a temperate deciduous forest. *Tree Physiology* 23: 517–525.
- Bachofen C, D'Odorico P, Buchmann N. 2020. Light and VPD gradients drive foliar nitrogen partitioning and photosynthesis in the canopy of European beech and silver fir. *Oecologia* 192: 323–339.
- Baker NR. 2008. Chlorophyll fluorescence: a probe of photosynthesis *in vivo*. *Annual Review of Plant Biology* 59: 89–113.
- Baldocchi DD, Meyers TP. 1988. A spectral and lag-correlation analysis of turbulence in a deciduous forest canopy. *Boundary-Layer Meteorology* 45: 31–58.
- Baldocchi DD, Meyers TP. 1991. Trace gas exchange above the floor of a deciduous forest: 1. Evaporation and CO₂ efflux. *Journal of Geophysical Research: Atmospheres* 96: 7271–7285.
- Baldocchi DD, Vogel CA, Hall B. 1997. Seasonal variation of energy and water vapor exchange rates above and below a boreal jack pine forest canopy. *Journal of Geophysical Research: Atmospheres* 102: 28939–28951.
- Ball MC, Cowan IR, Farquhar GD. 1988. Maintenance of leaf temperature and the optimisation of carbon gain in relation to water loss in a tropical mangrove forest. *Functional Plant Biology* 15: 263–276.
- Baltzer JL, Thomas SC. 2005. Leaf optical responses to light and soil nutrient availability in temperate deciduous trees. *American Journal of Botany* 92: 214–223.
- Banerjee T, De Roo F, Mauder M. 2017. Explaining the convective effect in canopy turbulence by means of large-eddy simulation. *Hydrology and Earth System Sciences* 21: 2987–3000.
- Banerjee T, Linn R. 2018. Effect of vertical canopy architecture on transpiration, thermoregulation and carbon assimilation. *Forests* 9: 198.
- Barnard DM, Bauerle WL. 2016. Seasonal variation in canopy aerodynamics and the sensitivity of transpiration estimates to wind velocity in broadleaved deciduous species. *Journal of Hydrometeorology* 17: 3029–3043.
- Bartemucci P, Messier C, Canham CD. 2006. Overstory influences on light attenuation patterns and understory plant community diversity and composition in southern boreal forests of Quebec. *Canadian Journal of Forest Research* 36: 2065–2079.
- Bartholomew DC, Bittencourt PRL, da Costa ACL, Banin LF, Costa PB, Coughlin SI, Domingues TF, Ferreira LV, Giles A, Mencuccini M *et al.* 2020. Small tropical forest trees have a greater capacity to adjust carbon metabolism to long-term drought than large canopy trees. *Plant, Cell & Environment* 43: 2380–2393.
- Béland M, Baldocchi DD. 2021. Vertical structure heterogeneity in broadleaf forests: effects on light interception and canopy photosynthesis. *Agricultural and Forest Meteorology* 307: 108525.
- Bennett AC, Arndt SK, Bennett LT, Knauer J, Beringer J, Griebel A, Hinko-Najera N, Liddell MJ, Metzen D, Pendall E *et al.* 2021. Thermal optima of gross primary productivity are closely aligned with mean air temperatures across Australian wooded ecosystems. *Global Change Biology* 27: 4727–4744.
- Bennett AC, McDowell NG, Allen CD, Anderson-Teixeira KJ. 2015. Larger trees suffer most during drought in forests worldwide. *Nature Plants* 1: 15139.
- Bertrand R, Aubret F, Grenouillet G, Ribéron A, Blanchet S. 2020. Comment on 'Forest microclimate dynamics drive plant responses to warming'. *Science* 370: 1–2.
- Bin Y, Li Y, Russo SE, Cao H, Ni Y, Ye W, Lian J. 2022. Leaf trait expression varies with tree size and ecological strategy in a subtropical forest. *Functional Ecology* 36: 1010–1022.
- Boardman NK. 1977. Comparative photosynthesis of sun and shade plants. *Annual Review of Plant Physiology* 28: 355–377.
- Bolstad PV, Mitchell K, Vose JM. 1999. Foliar temperature–respiration response functions for broad-leaved tree species in the southern Appalachians. *Tree Physiology* 19: 871–878.
- Bonan GB. 2016. *Ecological climatology: concepts and applications*. New York, NY, USA: Cambridge University Press.
- Bonan GB, Levis S, Sitch S, Vertenstein M, Oleson KW. 2003. A dynamic global vegetation model for use with climate models: concepts and description of simulated vegetation dynamics. *Global Change Biology* 9: 1543–1566.
- Bonan GB, Patton EG, Finnigan JJ, Baldocchi DD, Harman TN. 2021. Moving beyond the incorrect but useful paradigm: reevaluating big-leaf and multilayer

- plant canopies to model biosphere-atmosphere fluxes – a review. *Agricultural and Forest Meteorology* 306: 108435.
- Bonan GB, Patton EG, Harman IN, Oleson KW, Finnigan JJ, Lu Y, Burakowski EA. 2018. Modeling canopy-induced turbulence in the Earth system: a unified parameterization of turbulent exchange within plant canopies and the roughness sublayer (CLM-ml V0). *Geoscientific Model Development* 11: 1467–1496.
- Brando PM, Balch JK, Nepstad DC, Morton DC, Putz FE, Coe MT, Silvério D, Macedo MN, Davidson EA, Nóbrega CC *et al.* 2014. Abrupt increases in Amazonian tree mortality due to drought–fire interactions. *Proceedings of the National Academy of Sciences, USA* 111: 6347–6352.
- Breshears DD, Fontaine JB, Ruthrof KX, Field JP, Feng X, Burger JR, Law DJ, Kala J, Hardy GESJ. 2021. Underappreciated plant vulnerabilities to heat waves. *New Phytologist* 231: 32–39.
- Brooks JR, Flanagan LB, Varney GT, Ehleringer JR. 1997. Vertical gradients in photosynthetic gas exchange characteristics and refixation of respired CO₂ within boreal forest canopies. *Tree Physiology* 17: 1–12.
- Buckley TN. 2021. Optimal carbon partitioning helps reconcile the apparent divergence between optimal and observed canopy profiles of photosynthetic capacity. *New Phytologist* 230: 2246–2260.
- Buckley TN, Martorell S, Diaz-Espejo A, Tomás M, Medrano H. 2014. Is stomatal conductance optimized over both time and space in plant crowns? A field test in grapevine (*Vitis vinifera*). *Plant, Cell & Environment* 37: 2707–2721.
- Burgess SSO, Dawson TE, Burgess SSO. 2006. Regressions of leaf traits. *New Phytologist* 174: 626–636.
- Campbell G, Norman J. 1998. *An introduction to environmental biophysics*. New York, NY, USA: Springer.
- Carswell FE, Meir P, Wandelli EV, Bonates LCM, Kruijt B, Barbosa EM, Nobre AD, Grace J, Jarvis PG. 2000. Photosynthetic capacity in a central Amazonian rain forest. *Tree Physiology* 20: 179–186.
- Carter KR, Cavaleri MA. 2018. Within-canopy experimental leaf warming induces photosynthetic decline instead of acclimation in two northern hardwood species. *Frontiers in Forests and Global Change* 1: 1–17.
- Carter KR, Wood TE, Reed SC, Butts KM, Cavaleri MA. 2021. Experimental warming across a tropical forest canopy height gradient reveals minimal photosynthetic and respiratory acclimation. *Plant, Cell & Environment* 44: 2879–2897.
- de Casas RR, Vargas P, Pérez-Corona E, Manrique E, García-Verdugo C, Balaguer L. 2011. Sun and shade leaves of *Olea europaea* respond differently to plant size, light availability and genetic variation. *Functional Ecology* 25: 802–812.
- de Castro F. 2000. Light spectral composition in a tropical forest: measurements and model. *Tree Physiology* 20: 49–56.
- Cavaleri MA, Oberbauer SF, Clark DB, Clark DA, Ryan MG. 2010. Height is more important than light in determining leaf morphology in a tropical forest. *Ecology* 91: 1730–1739.
- Cavaleri MA, Oberbauer SF, Ryan MG. 2008. Foliar and ecosystem respiration in an old-growth tropical rain forest. *Plant, Cell & Environment* 31: 473–483.
- Cavender-Bares J, Bazzaz FA. 2000. Changes in drought response strategies with ontogeny in *Quercus rubra*: implications for scaling from seedlings to mature trees. *Oecologia* 124: 8–18.
- Chazdon RL, Fetcher N. 1984. Photosynthetic light environments in a lowland tropical rain forest in Costa Rica. *Journal of Ecology* 72: 553–564.
- Chen X, Massman WJ, Su Z. 2019. A column canopy-air turbulent diffusion method for different canopy structures. *Journal of Geophysical Research: Atmospheres* 124: 488–506.
- Chen X, Sun J, Wang M, Lyu M, Niklas KJ, Michaletz ST, Zhong Q, Cheng D. 2020. The leaf economics spectrum constrains phenotypic plasticity across a light gradient. *Frontiers in Plant Science* 11: 1–11.
- Chin ARO, Sillett SC. 2017. Leaf acclimation to light availability supports rapid growth in tall *Picea sitchensis* trees. *Tree Physiology* 37: 1352–1366.
- Chitra-Tarak R, Xu C, Aguilar S, Anderson-Teixeira KJ, Chambers J, Detto M, Faybishenko B, Fisher RA, Knox RG, Koven CD *et al.* 2021. Hydraulically-vulnerable trees survive on deep-water access during droughts in a tropical forest. *New Phytologist* 231: 1798–1813.
- Christoffersen BO, Gloor M, Fauset S, Fyllas NM, Galbraith DR, Baker R, Kruijt B, Rowland L, Fisher RA, Binks OJ *et al.* 2016. Linking hydraulic traits to tropical forest function in a size-structured and trait-driven model (TFS v.1-Hydro). *Geoscientific Model Development* 9: 4227–4255.
- Coble AP, Cavaleri MA. 2014. Light drives vertical gradients of leaf morphology in a sugar maple (*Acer saccharum*) forest. *Tree Physiology* 34: 146–158.
- Coble AP, VanderWall B, Mau A, Cavaleri MA. 2016. How vertical patterns in leaf traits shift seasonally and the implications for modeling canopy photosynthesis in a temperate deciduous forest. *Tree Physiology* 36: 1077–1091.
- Condit R, Watts K, Bohlman SA, Pérez R, Foster RB, Hubbell SP. 2000. Quantifying the deciduousness of tropical forest canopies under varying climates. *Journal of Vegetation Science* 11: 649–658.
- Copolovici LO, Filella I, Llusià J, Niinemets Ü, Peñuelas J. 2005. The capacity for thermal protection of photosynthetic electron transport varies for different monoterpenes in *Quercus ilex*. *Plant Physiology* 139: 485–496.
- Corlett RT. 2011. Impacts of warming on tropical lowland rainforests. *Trends in Ecology & Evolution* 26: 606–613.
- Couvreur V, Ledder G, Manzoni S, Way DA, Muller EB, Russo SE. 2018. Water transport through tall trees: a vertically explicit, analytical model of xylem hydraulic conductance in stems. *Plant, Cell & Environment* 41: 1821–1839.
- Cunningham SC, Read J. 2003. Do temperate rainforest trees have a greater ability to acclimate to changing temperatures than tropical rainforest trees? *New Phytologist* 157: 55–64.
- Curtis EM, Knight CA, Leigh A. 2019. Intracanopy adjustment of leaf-level thermal tolerance is associated with microclimatic variation across the canopy of a desert tree (*Acacia papyrocarpa*). *Oecologia* 189: 37–46.
- Dang QL, Margolis HA, Sy M, Coyea MR, Collatz GJ, Walthall CL. 1997. Profiles of photosynthetically active radiation, nitrogen and photosynthetic capacity in the boreal forest: implications for scaling from leaf to canopy. *Journal of Geophysical Research: Atmospheres* 102: 28845–28859.
- Davis FW, Synes NW, Fricker GA, McCullough IM, Serra-Diaz JM, Franklin J, Flint AL. 2019. LiDAR-derived topography and forest structure predict fine-scale variation in daily surface temperatures in oak savanna and conifer forest landscapes. *Agricultural and Forest Meteorology* 269–270: 192–202.
- De Frenne P, Lenoir J, Luoto M, Scheffers BR, Zellweger F, Aalto J, Ashcroft MB, Christiansen DM, Decocq G, Pauw KD *et al.* 2021. Forest microclimates and climate change: importance, drivers and future research agenda. *Global Change Biology* 27: 2279–2297.
- De Pury DGG, Farquhar GD. 1997. Simple scaling of photosynthesis from leaves to canopies without the errors of big-leaf models. *Plant, Cell & Environment* 20: 537–557.
- Denmead OT, Bradley EF. 1987. On scalar transport in plant canopies. *Irrigation Science* 8: 131–149.
- Detto M, Asner GP, Muller-Landau HC, Sonnentag O. 2015. Spatial variability in tropical forest leaf area density from multireturn lidar and modeling. *Journal of Geophysical Research – Biogeosciences* 120: 294–309.
- Dietz J, Leuschner C, Höltscher D, Kreilein H. 2007. Vertical patterns and duration of surface wetness in an old-growth tropical montane forest, Indonesia. *Flora – Morphology, Distribution, Functional Ecology of Plants* 202: 111–117.
- Domingues TF, Berry JA, Martinelli LA, Ometto JPHB, Ehleringer JR. 2005. Parameterization of canopy structure and leaf-level gas exchange for an eastern Amazonian tropical rain forest (Tapajós National Forest, Pará, Brazil). *Earth Interactions* 9: 1–23.
- Doughty CE, Goulden ML. 2008. Are tropical forests near a high temperature threshold? *Journal of Geophysical Research – Biogeosciences* 113: 1–12.
- Drake JE, Harwood R, Vårhammar A, Barbour MM, Reich PB, Barton CVM, Tjoelker MG. 2020. No evidence of homeostatic regulation of leaf temperature in *Eucalyptus parramattensis* trees: integration of CO₂ flux and oxygen isotope methodologies. *New Phytologist* 228: 1511–1523.
- Duque A, Stevenson PR, Feeley KJ. 2015. Thermophilization of adult and juvenile tree communities in the northern tropical Andes. *Proceedings of the National Academy of Sciences, USA* 112: 10744–10749.
- Duursma RA, Marshall JD. 2006. Vertical canopy gradients in $\delta^{13}\text{C}$ correspond with leaf nitrogen content in a mixed-species conifer forest. *Trees* 20: 496–506.
- Fauset S, Freitas HC, Galbraith DR, Sullivan MJP, Aidar MPM, Joly CA, Phillips OL, Vieira SA, Gloor MU. 2018. Differences in leaf thermoregulation and water use strategies between three co-occurring Atlantic forest tree species. *Plant, Cell & Environment* 41: 1618–1631.
- Feeley K, Martinez-Villa J, Perez T, Silva Duque A, Triviño Gonzalez D, Duque A. 2020. The thermal tolerances, distributions, and performances of tropical montane tree species. *Frontiers in Forests and Global Change* 3: 5–9.

- Field C. 1983. Allocating leaf nitrogen for the maximization of carbon gain: leaf age as a control on the allocation program. *Oecologia* 56: 341–347.
- Finnigan JJ. 1979. Turbulence in waving wheat. *Boundary-Layer Meteorology* 16: 181–211.
- Fisher JB, Lee B, Purdy AJ, Halverson GH, Dohlen MB, Cawse-Nicholson K, Wang A, Anderson RG, Aragon B, Arain MA *et al.* 2020. ECOSTRESS: NASA's next generation mission to measure evapotranspiration from the International Space Station. *Water Resources Research* 56: e2019WR026058.
- Fisher RA, Koven CD. 2020. Perspectives on the future of land surface models and the challenges of representing complex terrestrial systems. *Journal of Advances in Modeling Earth Systems* 12: e2018MS001453.
- Fisher RA, Koven CD, Anderegg WRL, Christoffersen BO, Dietze MC, Farrior CE, Holm JA, Hurtt GC, Knox RG, Lawrence PJ *et al.* 2018. Vegetation demographics in Earth system models: a review of progress and priorities. *Global Change Biology* 24: 35–54.
- Flores BM, Holmgren M, Xu C, van Nes EH, Jakovac CC, Mesquita RCG, Scheffer M. 2017. Floodplains as an Achilles' heel of Amazonian forest resilience. *Proceedings of the National Academy of Sciences, USA* 114: 4442–4446.
- Foley JA, Prentice IC, Ramankutty N, Levis S, Pollard D, Sitch S, Haxeltine A. 1996. An integrated biosphere model of land surface processes, terrestrial carbon balance, and vegetation dynamics. *Global Biogeochemical Cycles* 10: 603–628.
- Fredeen AL, Sage RF. 1999. Temperature and humidity effects on branchlet gas-exchange in white spruce: an explanation for the increase in transpiration with branchlet temperature. *Trees* 14: 161–168.
- Friedlingstein P, Cox P, Betts R, Bopp L, von Bloh W, Brovkin V, Cadule P, Doney S, Eby M, Fung I *et al.* 2006. Climate–carbon cycle feedback analysis: results from the C4MIP model intercomparison. *Journal of Climate* 19: 3337–3353.
- Fritts HC. 1976. *Tree rings and climate*. London, UK; New York, NY, USA: Academic Press.
- Garcia MN, Ferreira MJ, Ivanov V, dos Santos VAHF, Ceron JV, Guedes AV, Saleska SR, Oliveira RS. 2021. Importance of hydraulic strategy trade-offs in structuring response of canopy trees to extreme drought in central Amazon. *Oecologia* 197: 13–24.
- García-Plazaola JJ, Becerril JM, Hernández A, Niinemets Ü, Kollist H. 2004. Acclimation of antioxidant pools to the light environment in a natural forest canopy. *New Phytologist* 163: 87–97.
- Gebauer R, Volarik D, Urban J, Børja I, Nagy NE, Eldhuset TD, Krokene P. 2015. Effects of prolonged drought on the anatomy of sun and shade needles in young Norway spruce trees. *Ecology and Evolution* 5: 4989–4998.
- Gillerot L, Forrester DI, Bottero A, Rigling A, Lévesque M. 2020. Tree neighbourhood diversity has negligible effects on drought resilience of European beech, silver fir and Norway spruce. *Ecosystems* 24: 20–36.
- Gora EM, Esquivel-Muelbert A. 2021. Implications of size-dependent tree mortality for tropical forest carbon dynamics. *Nature Plants* 7: 384–391.
- Goss R, Lepetit B. 2015. Biodiversity of NPQ. *Journal of Plant Physiology* 172: 13–32.
- Gregoriou K, Pontikis K, Vemmos S. 2007. Effects of reduced irradiance on leaf morphology, photosynthetic capacity, and fruit yield in olive (*Olea europaea* L.). *Photosynthetica* 45: 172–181.
- Greiser C, Ehrlén J, Meineri E, Hylander K. 2019. Hiding from the climate: characterizing microrefugia for boreal forest understory species. *Global Change Biology* 26: 471–483.
- Grossiord C, Buckley TN, Cernusak LA, Novick KA, Poulter B, Siegwolf RTW, Sperry JS, McDowell NG. 2020. Plant responses to rising vapor pressure deficit. *New Phytologist* 226: 1550–1566.
- Haberlandt G. 1914. *Physiological plant anatomy*. London, UK: Macmillan & Co.
- Hadley JL, Smith WK. 1987. Influence of krummholz mat microclimate on needle physiology and survival. *Oecologia* 73: 82–90.
- Haesen S, Lembrechts JJ, De Frenne P, Lenoir J, Aalto J, Ashcroft MB, Kopecký M, Luoto M, Maclean I, Nijs I *et al.* 2021. ForestTemp – sub-canopy microclimate temperatures of European forests. *Global Change Biology* 27: 6307–6319.
- Hamerlynck E, Knapp AK. 1996. Photosynthetic and stomatal responses to high temperature and light in two oaks at the western limit of their range. *Tree Physiology* 16: 557–565.
- Hanberry BB, Bragg DC, Alexander HD. 2020. Open forest ecosystems: an excluded state. *Forest Ecology and Management* 472: 118256.
- Hanberry BB, Bragg DC, Hutchinson TF. 2018. A reconceptualization of open oak and pine ecosystems of eastern North America using a forest structure spectrum. *Ecosphere* 9: e02431.
- Hansen U, Fiedler B, Rank B. 2002. Variation of pigment composition and antioxidative systems along the canopy light gradient in a mixed beech/oak forest: a comparative study on deciduous tree species differing in shade tolerance. *Trees* 16: 354–364.
- Hardwick SR, Toumi R, Pfeifer M, Turner EC, Nilus R, Ewers RM. 2015. The relationship between leaf area index and microclimate in tropical forest and oil palm plantation: forest disturbance drives changes in microclimate. *Agricultural and Forest Meteorology* 201: 187–195.
- Harley P, Guenther A, Zimmerman P. 1996. Effects of light, temperature and canopy position on net photosynthesis and isoprene emission from sweetgum (*Liquidambar styraciflua*) leaves. *Tree Physiology* 16: 25–32.
- Harley P, Guenther A, Zimmerman P. 1997. Environmental controls over isoprene emission in deciduous oak canopies. *Tree Physiology* 17: 705–714.
- Harman IN, Finnigan JJ. 2007. A simple unified theory for flow in the canopy and roughness sublayer. *Boundary-Layer Meteorology* 123: 339–363.
- Harris NL, Medina E. 2013. Changes in leaf properties across an elevation gradient in the Luquillo Mountains, Puerto Rico. *Ecological Bulletins* 54: 169–180.
- He L, Chen JM, Gonsamo A, Luo X, Wang R, Liu Y, Liu R. 2018. Changes in the shadow: the shifting role of shaded leaves in global carbon and water cycles under climate change. *Geophysical Research Letters* 45: 5052–5061.
- Heilman KA, Dietze MC, Arizpe AA, Aragon J, Gray A, Shaw JD, Finley AO, Klesse S, DeRose RJ, Evans MEK. 2022. Ecological forecasting of tree growth: regional fusion of tree-ring and forest inventory data to quantify drivers and characterize uncertainty. *Global Change Biology* 28: 2442–2460.
- Hernández GG, Winter K, Slot M. 2020. Similar temperature dependence of photosynthetic parameters in sun and shade leaves of three tropical tree species. *Tree Physiology* 40: 637–651.
- Hikosaka K. 2014. Optimal nitrogen distribution within a leaf canopy under direct and diffuse light. *Plant, Cell & Environment* 37: 2077–2085.
- Hirose T, Werger MJA. 1987. Maximizing daily canopy photosynthesis with respect to the leaf nitrogen allocation pattern in the canopy. *Oecologia* 72: 520–526.
- Hogan JA, McMahon SM, Buzzard V, Michaletz ST, Enquist BJ, Thompson J, Swenson NG, Zimmerman JK. 2019. Drought and the interannual variability of stem growth in an aseasonal, everwet forest. *Biotropica* 51: 139–154.
- Houter NC, Pons TL. 2012. Ontogenetic changes in leaf traits of tropical rainforest trees differing in juvenile light requirement. *Oecologia* 169: 33–45.
- Huang M, Piao S, Ciais P, Peñuelas J, Wang X, Keenan TF, Peng S, Berry JA, Wang K, Mao J *et al.* 2019. Air temperature optima of vegetation productivity across global biomes. *Nature Ecology & Evolution* 3: 772–779.
- Hulley G, Shivers S, Wetherley E, Cudd R. 2019. New ECOSTRESS and MODIS land surface temperature data reveal fine-scale heat vulnerability in cities: a case study for Los Angeles County, California. *Remote Sensing* 11: 2136.
- Humphrey V, Berg A, Ciais P, Gentile P, Jung M, Reichstein M, Seneviratne SI, Frankenberg C. 2021. Soil moisture–atmosphere feedback dominates land carbon uptake variability. *Nature* 592: 65–69.
- Hurtt GC, Moorcroft PR, Levin SA. 1998. Terrestrial models and global change: challenges for the future. *Global Change Biology* 4: 581–590.
- Ichie T, Inoue Y, Takahashi N, Kamiya K, Kenzo T. 2016. Ecological distribution of leaf stomata and trichomes among tree species in a Malaysian lowland tropical rain forest. *Journal of Plant Research* 129: 625–635.
- IPCC. 2021. *Climate change 2021 the physical science basis–IPCC*. Cambridge, UK: Cambridge University Press, 1–3949.
- Irvine J, Law BE, Kurpius MR, Anthoni PM, Moore D, Schwarz PA. 2004. Age-related changes in ecosystem structure and function and effects on water and carbon exchange in ponderosa pine. *Tree Physiology* 24: 753–763.
- Ishida A, Toma T, Marjenah M. 1999. Leaf gas exchange and chlorophyll fluorescence in relation to leaf angle, azimuth, and canopy position in the tropical pioneer tree *Macaranga conferta*. *Tree Physiology* 19: 117–124.
- Jiao-jun Z, Xiu-fen L, Yutaka G, Takeshi M. 2004. Wind profiles in and over trees. *Journal of Forestry Research* 15: 305.

- Johnston MR, Andreu A, Verfaillie J, Baldocchi D, Moorcroft PR. 2022. What lies beneath: vertical temperature heterogeneity in a Mediterranean woodland savanna. *Remote Sensing of Environment* 274: 112950.
- Jones SM, Bottero A, Kastendick DN, Palik BJ. 2019. Managing red pine stand structure to mitigate drought impacts. *Dendrochronologia* 57: 125623.
- Jucker T, Hardwick SR, Both S, Elias DMO, Ewers RM, Milodowski DT, Swinfield T, Coomes DA. 2018. Canopy structure and topography jointly constrain the microclimate of human-modified tropical landscapes. *Global Change Biology* 24: 5243–5258.
- Kafuti C, Bourland N, De Mil T, Meeus S, Rousseau M, Toirambe B, Bolaluembe P-C, Ndjele L, Beekman H. 2020. Foliar and wood traits covary along a vertical gradient within the crown of long-lived light-demanding species of the Congo Basin semi-deciduous forest. *Forests* 11: 35.
- Katul GG, Albertson JD. 1999. Modeling CO₂ sources, sinks, and fluxes within a forest canopy. *Journal of Geophysical Research: Atmospheres* 104: 6081–6091.
- Keenan TF, Niinemets Ü. 2016. Global leaf trait estimates biased due to plasticity in the shade. *Nature Plants* 3: 1–6.
- Kenzo T, Inoue Y, Yoshimura M, Yamashita M, Tanaka-Oda A, Ichie T. 2015. Height-related changes in leaf photosynthetic traits in diverse Bornean tropical rain forest trees. *Oecologia* 177: 191–202.
- Kesselmeier J, Staudt M. 1999. Biogenic volatile organic compounds (VOC): an overview on emission, physiology and ecology. *Journal of Atmospheric Chemistry* 33: 23–88.
- Kikuzawa K, Lechowicz MJ. 2006. Toward synthesis of relationships among leaf longevity, instantaneous photosynthetic rate, lifetime leaf carbon gain, and the gross primary production of forests. *The American Naturalist* 168: 373–383.
- Kitao M, Kitaoka S, Komatsu M, Utsugi H, Tobita H, Koike T, Maruyama Y. 2012. Leaves of Japanese oak (*Quercus mongolica* var. *crispula*) mitigate photoinhibition by adjusting electron transport capacities and thermal energy dissipation along the intra-canopy light gradient. *Physiologia Plantarum* 146: 192–204.
- Knapp AK, Carter GA. 1998. Variability in leaf optical properties among 26 species from a broad range of habitats. *American Journal of Botany* 85: 940–946.
- Koch GW, Amthor JS, Goulden ML. 1994. Diurnal patterns of leaf photosynthesis, conductance and water potential at the top of a lowland rain forest canopy in Cameroon: measurements from the Radeau des Cimes. *Tree Physiology* 14: 347–360.
- Koch GW, Sillett SC, Jennings GM, Davis SD. 2004. The limits to tree height. *Nature* 428: 851–854.
- Koike F, Syahbuddin. 1993. Canopy structure of a tropical rain forest and the nature of an unstratified upper layer. *Functional Ecology* 7: 230–235.
- Koike T, Kitao M, Maruyama Y, Mori S, Lei TT. 2001. Leaf morphology and photosynthetic adjustments among deciduous broad-leaved trees within the vertical canopy profile. *Tree Physiology* 21: 951–958.
- Königer M, Harris GC, Virgo A, Winter K. 1995. Xanthophyll-cycle pigments and photosynthetic capacity in tropical forest species: a comparative field study on canopy, gap and understory plants. *Oecologia* 104: 280–290.
- Konrad W, Katul G, Roth-Nebelsick A. 2021. Leaf temperature and its dependence on atmospheric CO₂ and leaf size. *Geological Journal* 56: 866–885.
- Kosugi Y, Matsuo N. 2006. Seasonal fluctuations and temperature dependence of leaf gas exchange parameters of co-occurring evergreen and deciduous trees in a temperate broad-leaved forest. *Tree Physiology* 26: 1173–1184.
- Kosugi Y, Takanashi S, Yokoyama N, Philip E, Kamakura M. 2012. Vertical variation in leaf gas exchange parameters for a Southeast Asian tropical rainforest in Peninsular Malaysia. *Journal of Plant Research* 125: 735–748.
- Krause A, Pugh TAM, Bayer AD, Li W, Leung F, Bondeau A, Doelman JC, Humpenöder F, Anthoni P, Bodirsky BL *et al.* 2018. Large uncertainty in carbon uptake potential of land-based climate-change mitigation efforts. *Global Change Biology* 24: 3025–3038.
- Krause GH, Winter K, Krause B, Jahns P, García M, Aranda J, Virgo A. 2010. High-temperature tolerance of a tropical tree, *Ficus insipida*: methodological reassessment and climate change considerations. *Functional Plant Biology* 37: 890.
- Krinner G, Viovy N, de Noblet-Ducoudré N, Ogée J, Polcher J, Friedlingstein P, Ciais P, Sitch S, Prentice IC. 2005. A dynamic global vegetation model for studies of the coupled atmosphere-biosphere system. *Global Biogeochemical Cycles* 19: 1–25.
- Kumarathunge DP, Medlyn BE, Drake JE, Tjoelker MG, Aspinwall MJ, Battaglia M, Cano FJ, Carter KR, Cavaleri MA, Cernusak LA *et al.* 2019. Acclimation and adaptation components of the temperature dependence of plant photosynthesis at the global scale. *New Phytologist* 222: 768–784.
- Kunert N, Aparecido LMT, Wolff S, Higuchi N, dos Santos J, de Araujo AC, Trumbore S. 2017. A revised hydrological model for the central Amazon: the importance of emergent canopy trees in the forest water budget. *Agricultural and Forest Meteorology* 239: 47–57.
- Kunert N, Hajek P, Hietz P, Morris H, Rosner S, Tholen D. 2022. Summer temperatures reach the thermal tolerance threshold of photosynthetic decline in temperate conifers. *Plant Biology* 24: 1254–1261.
- Kusi J, Karsai I. 2020. Plastic leaf morphology in three species of *Quercus*: the more exposed leaves are smaller, more lobated and denser. *Plant Species Biology* 35: 24–37.
- Lantz AT, Allman J, Weraduwaage SM, Sharkey TD. 2019. Isoprene: new insights into the control of emission and mediation of stress tolerance by gene expression. *Plant, Cell & Environment* 42: 2808–2826.
- Laohawornkitkul J, Taylor JE, Paul ND, Hewitt CN. 2009. Biogenic volatile organic compounds in the Earth system. *New Phytologist* 183: 27–51.
- Laurance WF, Nascimento HEM, Laurance SG, Andrade AC, Fearnside PM, Ribeiro JEL, Capretz RL. 2006. Rain forest fragmentation and the proliferation of successional trees. *Ecology* 87: 469–482.
- Law BE, Cescatti A, Baldocchi DD. 2001. Leaf area distribution and radiative transfer in open-canopy forests: implications for mass and energy exchange. *Tree Physiology* 21: 777–787.
- Lee BR, Ibáñez I. 2021. Spring phenological escape is critical for the survival of temperate tree seedlings. *Functional Ecology* 35: 1848–1861.
- Lee DW, Bone RA, Tarsis SL, Storch D. 1990. Correlates of leaf optical properties in tropical forest sun and extreme-shade plants. *American Journal of Botany* 77: 370–380.
- Legner N, Fleck S, Leuschner C. 2014. Within-canopy variation in photosynthetic capacity, SLA and foliar N in temperate broad-leaved trees with contrasting shade tolerance. *Trees* 28: 263–280.
- Leigh A, Sevanto S, Close JD, Nicotra AB. 2017. The influence of leaf size and shape on leaf thermal dynamics: does theory hold up under natural conditions? *Plant, Cell & Environment* 40: 237–248.
- Levizou E, Drilias P, Psaras GK, Manetas Y. 2005. Nondestructive assessment of leaf chemistry and physiology through spectral reflectance measurements may be misleading when changes in trichome density co-occur. *New Phytologist* 165: 463–472.
- Liakoura V, Stefanou M, Manetas Y, Cholevas C, Karabourniotis G. 1997. Trichome density and its UV-B protective potential are affected by shading and leaf position on the canopy. *Environmental and Experimental Botany* 38: 223–229.
- Lloyd J, Farquhar GD. 2008. Effects of rising temperatures and [CO₂] on the physiology of tropical forest trees. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 363: 1811–1817.
- Lloyd J, Patiño S, Paiva RQ, Nardoto GB, Quesada CA, Santos AJB, Baker TR, Brand WA, Hilke I, Gielmann H *et al.* 2010. Optimisation of photosynthetic carbon gain and within-canopy gradients of associated foliar traits for Amazon forest trees. *Biogeosciences* 7: 1833–1859.
- Longo M, Knox RG, Medvigy DM, Levine NM, Dietze MC, Kim Y, Swann ALS, Zhang K, Rollinson CR, Bras RL *et al.* 2019. The biophysics, ecology, and biogeochemistry of functionally diverse, vertically and horizontally heterogeneous ecosystems: the ecosystem demography model, v.2.2 – part 1: model description. *Geoscientific Model Development* 12: 4309–4346.
- Lowman M, Rinker HB. 1995. *Forest canopies*. Cambridge, MA, USA: Academic Press.
- Lusk CH, Reich PB, Montgomery RA, Ackerly DD, Cavender-Bares J. 2008. Why are evergreen leaves so contrary about shade? *Trends in Ecology & Evolution* 23: 299–303.
- Maes SL, Perring MP, Depauw L, Bernhardt-Römermann M, Blondeel H, Brümelis G, Brunet J, Decocq G, den Ouden J, Govaert S *et al.* 2020. Plant functional trait response to environmental drivers across European temperate forest understorey communities. *Plant Biology* 22: 410–424.
- Maclean IMD, Klings DH. 2021. Microclim: a mechanistic model of above, below and within-canopy microclimate. *Ecological Modelling* 451: 109567.

- Majasalmi T, Rautiainen M. 2020. The impact of tree canopy structure on understory variation in a boreal forest. *Forest Ecology and Management* 466: 118100.
- Marenco RA, Camargo MAB, Antezana-Vera SA, Oliveira MF. 2017. Leaf trait plasticity in six forest tree species of central Amazonia. *Photosynthetica* 55: 679–688.
- Martin TA, Hinckley TM, Meinzer FC, Sprugel DG. 1999. Boundary layer conductance, leaf temperature and transpiration of *Abies amabilis* branches. *Tree Physiology* 19: 435–443.
- Matsubara S, Krause GH, Aranda J, Virgo A, Beisel KG, Jahns P, Winter K, Matsubara S, Krause GH, Aranda J *et al.* 2009. Sun-shade patterns of leaf carotenoid composition in 86 species of neotropical forest plants. *Functional Plant Biology* 36: 20–36.
- Matusick G, Ruthrof KX, Brouwers NC, Dell B, Hardy GSJ. 2013. Sudden forest canopy collapse corresponding with extreme drought and heat in a mediterranean-type eucalypt forest in southwestern Australia. *European Journal of Forest Research* 132: 497–510.
- Mau A, Reed S, Wood T, Cavaleri M. 2018. Temperate and tropical forest canopies are already functioning beyond their thermal thresholds for photosynthesis. *Forests* 9: 47.
- McDowell NG, Allen CD, Anderson-Teixeira K, Aukema BH, Bond-Lamberty B, Chini L, Clark JS, Dietze M, Grossiord C, Hanbury-Brown A *et al.* 2020. Pervasive shifts in forest dynamics in a changing world. *Science* 368: eaaz9463.
- McDowell NG, Bond BJ, Hill L, Ryan MG, Whitehead D. 2011. Relationship between tree height and carbon isotope discrimination. In: Meinzer FC, Niinemets U, eds. *Size and age related changes in tree structure and function*. New York, NY, USA: Springer, 255–286.
- McGregor IR, Helcoski R, Kunert N, Tepley AJ, Gonzalez-Akre EB, Herrmann V, Zailaa J, Stovall AEL, Bourg NA, McShea WJ *et al.* 2021. Tree height and leaf drought tolerance traits shape growth responses across droughts in a temperate broadleaf forest. *New Phytologist* 231: 601–616.
- Meakem V, Tepley AJ, Gonzalez-Akre EB, Herrmann V, Muller-Landau HC, Wright SJ, Hubbell SP, Condit R, Anderson-Teixeira KJ. 2018. Role of tree size in moist tropical forest carbon cycling and water deficit responses. *New Phytologist* 219: 947–958.
- Mediavilla S, Escudero A. 2004. Stomatal responses to drought of mature trees and seedlings of two co-occurring Mediterranean oaks. *Forest Ecology and Management* 187: 281–294.
- Mediavilla S, Martín I, Babiano J, Escudero A. 2019. Foliar plasticity related to gradients of heat and drought stress across crown orientations in three Mediterranean *Quercus* species. *PLoS ONE* 14: e0224462.
- Meehl GA, Tebaldi C. 2004. More intense, more frequent, and longer lasting heat waves in the 21st century. *Science* 305: 994–997.
- Meeussen C, Govaert S, Vanneste T, Bollmann K, Brunet J, Calders K, Cousins SAO, De Pauw K, Diekmann M, Gasperini C *et al.* 2021. Microclimatic edge-to-interior gradients of European deciduous forests. *Agricultural and Forest Meteorology* 311: 108699.
- Meinzer FC, Clearwater MJ, Goldstein G. 2001. Water transport in trees: current perspectives, new insights and some controversies. *Environmental and Experimental Botany* 45: 239–262.
- Meir P, Grace J, Miranda AC. 2021. Leaf respiration in two tropical rainforests: constraints on physiology by phosphorus, nitrogen and temperature. *Functional Ecology* 15: 378–387.
- Meyers TP, Paw UKT. 1987. Modelling the plant canopy micrometeorology with higher-order closure principles. *Agricultural and Forest Meteorology* 41: 143–163.
- Michaletz ST, Weiser MD, McDowell NG, Zhou J, Kaspari M, Helliker BR, Enquist BJ. 2016. The energetic and carbon economic origins of leaf thermoregulation. *Nature Plants* 2: 16129.
- Michaletz ST, Weiser MD, Zhou J, Kaspari M, Helliker BR, Enquist BJ. 2015. Plant thermoregulation: energetics, trait–environment interactions, and carbon economics. *Trends in Ecology & Evolution* 30: 714–724.
- Millen GGM, Clendon JHM. 1979. Leaf angle: an adaptive feature of sun and shade leaves. *Botanical Gazette* 140: 437–442.
- Miller AD, Thompson JR, Tepley AJ, Anderson-Teixeira KJ. 2019. Alternative stable equilibria and critical thresholds created by fire regimes and plant responses in a fire-prone community. *Ecography* 42: 55–66.
- Miller BD, Carter KR, Reed SC, Wood TE, Cavaleri MA. 2021. Only sun-lit leaves of the uppermost canopy exceed both air temperature and photosynthetic thermal optima in a wet tropical forest. *Agricultural and Forest Meteorology* 301–302: 108347.
- Miller SD, Goulden ML, Hutya LR, Keller M, Saleska SR, Wofsy SC, Figueira AMS, da Rocha HR, de Camargo PB. 2011. Reduced impact logging minimally alters tropical rainforest carbon and energy exchange. *Proceedings of the National Academy of Sciences, USA* 108: 19431–19435.
- Misson L, Baldocchi DD, Black TA, Blanken PD, Brunet Y, Curiel Yuste J, Dorsey JR, Falk M, Granier A, Irvine MR *et al.* 2007. Partitioning forest carbon fluxes with overstory and understory eddy-covariance measurements: a synthesis based on FLUXNET data. *Agricultural and Forest Meteorology* 144: 14–31.
- Monson RK, Weraduwa SM, Rosenkranz M, Schnitzler J-P, Sharkey TD. 2021. Leaf isoprene emission as a trait that mediates the growth-defense tradeoff in the face of climate stress. *Oecologia* 197: 885–902.
- Monteith JL, Unsworth MH. 2013. *Principles of environmental physics: plants, animals, and the atmosphere*. Amsterdam, the Netherlands; Boston, MA, USA: Elsevier/Academic Press.
- Moorcroft PR, Hurtt GC, Pacala SW. 2001. A method for scaling vegetation dynamics: the ecosystem demography model (ED). *Ecological Monographs* 71: 557–586.
- Moore G, Orozco G, Aparecido L, Miller G. 2018. Upscaling transpiration in diverse forests: insights from a tropical premontane site. *Ecophysiology* 11: e1920.
- Mott KA, Peak D. 2010. Stomatal responses to humidity and temperature in darkness. *Plant, Cell & Environment* 33: 1084–1090.
- Muir CD. 2019. TEALEAVES: an R package for modelling leaf temperature using energy budgets. *AoB PLANTS* 11: 1–8.
- Muller JD, Rotenberg E, Tatarinov F, Oz I, Yakir D. 2021. Evidence for efficient non-evaporative leaf-to-air heat dissipation in a pine forest under drought conditions. *New Phytologist* 232: 2254–2266.
- Muller-Landau HC, Condit RS, Chave J, Thomas SC, Bohlman SA, Bunyavechewin S, Davies S, Foster R, Gunatilleke S, Gunatilleke N *et al.* 2006. Testing metabolic ecology theory for allometric scaling of tree size, growth and mortality in tropical forests. *Ecology Letters* 9: 575–588.
- Musselman KN, Margulis SA, Molotch NP. 2013. Estimation of solar direct beam transmittance of conifer canopies from airborne LiDAR. *Remote Sensing of Environment* 136: 402–415.
- Nakamura A, Kitching RL, Cao M, Creedy TJ, Fayle TM, Freiberg M, Hewitt CN, Itioka T, Koh LP, Ma K *et al.* 2017. Forests and their canopies: achievements and horizons in canopy science. *Trends in Ecology & Evolution* 32: 438–451.
- Niinemets Ü. 1998. Adjustment of foliage structure and function to a canopy light gradient in two co-existing deciduous trees. Variability in leaf inclination angles in relation to petiole morphology. *Trees* 12: 446–451.
- Niinemets Ü. 2007. Photosynthesis and resource distribution through plant canopies. *Plant, Cell & Environment* 30: 1052–1071.
- Niinemets Ü. 2010. Responses of forest trees to single and multiple environmental stresses from seedlings to mature plants: past stress history, stress interactions, tolerance and acclimation. *Forest Ecology and Management* 260: 1623–1639.
- Niinemets Ü. 2016. Leaf age dependent changes in within-canopy variation in leaf functional traits: a meta-analysis. *Journal of Plant Research* 129: 313–338.
- Niinemets Ü, Bilger W, Kull O, Tenhunen JD. 1998. Acclimation to high irradiance in temperate deciduous trees in the field: changes in xanthophyll cycle pool size and in photosynthetic capacity along a canopy light gradient. *Plant, Cell & Environment* 21: 1205–1218.
- Niinemets U, Copolovici L, Hueve K. 2010. High within-canopy variation in isoprene emission potentials in temperate trees: implications for predicting canopy-scale isoprene fluxes. *Journal of Geophysical Research – Biogeosciences* 115: G04029.
- Niinemets Ü, Keenan TF, Hallik L. 2015a. A worldwide analysis of within-canopy variations in leaf structural, chemical and physiological traits across plant functional types. *New Phytologist* 205: 973–993.
- Niinemets Ü, Kull O, Tenhunen JD. 2015b. Variability in leaf morphology and chemical composition as a function of canopy light environment in coexisting deciduous trees. *International Journal of Plant Sciences* 205: 973–993.
- Niinemets Ü, Oja V, Kull O. 1999. Shape of leaf photosynthetic electron transport versus temperature response curve is not constant along canopy light gradients in temperate deciduous trees. *Plant, Cell & Environment* 22: 1497–1513.
- Niinemets Ü, Sonninen E, Tobias M. 2004. Canopy gradients in leaf intercellular CO₂ mole fractions revisited: interactions between leaf irradiance and water stress need consideration. *Plant, Cell & Environment* 27: 569–583.

- Niinemets Ü, Sun Z. 2015. How light, temperature, and measurement and growth [CO₂] interactively control isoprene emission in hybrid aspen. *Journal of Experimental Botany* 66: 841–851.
- Niinemets Ü, Valladares F. 2004. Photosynthetic acclimation to simultaneous and interacting environmental stresses along natural light gradients: optimality and constraints. *Plant Biology* 6: 254–268.
- Niyogi KK. 2000. Safety valves for photosynthesis. *Current Opinion in Plant Biology* 3: 455–460.
- Novick KA, Ficklin DL, Stoy PC, Williams CA, Bohrer G, Oishi AC, Papuga SA, Blanken PD, Noormets A, Sulman BN *et al.* 2016. The increasing importance of atmospheric demand for ecosystem water and carbon fluxes. *Nature Climate Change* 6: 1023–1027.
- Nunes MH, Camargo JLC, Vincent G, Calders K, Oliveira RS, Huete A, Mendes de Moura Y, Nelson B, Smith MN, Stark SC *et al.* 2022. Forest fragmentation impacts the seasonality of Amazonian evergreen canopies. *Nature Communications* 13: 1–10.
- O'Sullivan OS, Heskell MA, Reich PB, Tjoelker MG, Weerasinghe LK, Penillard A, Zhu L, Egerton JGG, Bloomfield KJ, Creek D *et al.* 2017. Thermal limits of leaf metabolism across biomes. *Global Change Biology* 23: 209–223.
- Oldham AR, Sillett SC, Tomescu AMF, Koch GW. 2010. The hydrostatic gradient, not light availability, drives height-related variation in *Sequoia sempervirens* (Cupressaceae) leaf anatomy. *American Journal of Botany* 97: 1087–1097.
- Olson ME, Soriano D, Rosell JA, Anfodillo T, Donoghue MJ, Edwards EJ, León-Gómez C, Dawson T, Martínez JJC, Castorena M *et al.* 2018. Plant height and hydraulic vulnerability to drought and cold. *Proceedings of the National Academy of Sciences, USA* 115: 7551–7556.
- Osada N, Takeda H, Furukawa A, Awang M. 2001. Leaf dynamics and maintenance of tree crowns in a Malaysian rain forest stand. *Journal of Ecology* 89: 774–782.
- Osnas JLD, Katabuchi M, Kitajima K, Wright SJ, Reich PB, Van Bael SA, Kraft NJB, Samaniego MJ, Pacala SW, Lichstein JW. 2018. Divergent drivers of leaf trait variation within species, among species, and among functional groups. *Proceedings of the National Academy of Sciences, USA* 115: 5480–5485.
- Ozanne CMP. 2003. Biodiversity meets the atmosphere: a global view of forest canopies. *Science* 301: 183–186.
- Parker GG, Fitzjarrald DR, Gonçalves Sampaio IC. 2019. Consequences of environmental heterogeneity for the photosynthetic light environment of a tropical forest. *Agricultural and Forest Meteorology* 278: 107661.
- Parker GG, O'Neill JP, Higman D. 1989. Vertical profile and canopy organization in a mixed deciduous forest. *Vegetatio* 85: 1–11.
- Pau S, Detto M, Kim Y, Still CJ. 2018. Tropical forest temperature thresholds for gross primary productivity. *Ecosphere* 9: e02311.
- Penman HL, Long IF. 1960. Weather in wheat: an essay in micro-meteorology. *Quarterly Journal of the Royal Meteorological Society* 86: 16–50.
- Perez TM, Feeley KJ. 2018. Increasing humidity threatens tropical rainforests. *Frontiers in Ecology and Evolution* 6: 68.
- Perez TM, Feeley KJ. 2020. Photosynthetic heat tolerances and extreme leaf temperatures. *Functional Ecology* 34: 2236–2245.
- Piponiot C, Anderson-Teixeira KJ, Davies SJ, Allen D, Bourg NA, Burslem DFRP, Cárdenas D, Chang-Yang C-H, Chuyong G, Cordell S *et al.* 2022. Distribution of biomass dynamics in relation to tree size in forests across the world. *New Phytologist* 234: 1664–1677.
- Poorter L, Kwant R, Hernández R, Medina E, Werger MJA. 2000. Leaf optical properties in Venezuelan cloud forest trees. *Tree Physiology* 20: 519–526.
- Poorter L, Oberbauer SF, Clark DB. 1995. Leaf optical properties along a vertical gradient in a tropical rain forest canopy in Costa Rica. *American Journal of Botany* 82: 1257–1263.
- Pörtner H-O, Scholes RJ, Agard J, Archer E, Arneth A, Bai X, Barnes D, Burrows M, Chan L, Cheung WL *et al.* 2021. *Scientific outcome of the IPBES-IPCC co-sponsored workshop on biodiversity and climate change*. Bonn, Germany: Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES), 1–234.
- Raupach MR. 1987. A Lagrangian analysis of scalar transfer in vegetation canopies. *Quarterly Journal of the Royal Meteorological Society* 113: 107–120.
- Raupach MR. 1989. Applying Lagrangian fluid mechanics to infer scalar source distributions from concentration profiles in plant canopies. *Agricultural and Forest Meteorology* 47: 85–108.
- Raupach MR, Shaw RH. 1982. Averaging procedures for flow within vegetation canopies. *Boundary-Layer Meteorology* 22: 79–90.
- Rey-Sánchez A, Slot M, Posada J, Kitajima K. 2016. Spatial and seasonal variation in leaf temperature within the canopy of a tropical forest. *Climate Research* 71: 75–89.
- Riedlmeier M, Ghirardo A, Wenig M, Knappe C, Koch K, Georgii E, Dey S, Parker JE, Schnitzler J-P, Vlot AC. 2017. Monoterpenes support systemic acquired resistance within and between plants. *Plant Cell* 29: 1440–1459.
- Rijkers T, Pons TL, Bongers F. 2000. The effect of tree height and light availability on photosynthetic leaf traits of four neotropical species differing in shade tolerance. *Functional Ecology* 14: 77–86.
- Roberts J, Cabral OMR, Aguiar LFD. 1990. Stomatal and boundary-layer conductances in an Amazonian terra firme rain forest. *Journal of Applied Ecology* 27: 336.
- Rohde RA, Hausfather Z. 2020. The Berkeley Earth land/ocean temperature record. *Earth System Science Data* 12: 3469–3479.
- Rollinson CR, Alexander MR, Dye AW, Moore DJP, Pederson N, Trouet V. 2020. Climate sensitivity of understory trees differs from overstory trees in temperate mesic forests. *Ecology* 102: e03264.
- Rozendaal DMA, Hurtado VH, Poorter L. 2006. Plasticity in leaf traits of 38 tropical tree species in response to light; relationships with light demand and adult stature. *Functional Ecology* 20: 207–216.
- Ruehr NK, Gast A, Weber C, Daub B, Arneth A. 2016. Water availability as dominant control of heat stress responses in two contrasting tree species. *Tree Physiology* 36: 164–178.
- Russell MB, Woodall CW, Fraver S, D'Amato AW, Domke GM, Skog KE. 2014. Residence times and decay rates of downed woody debris biomass/carbon in eastern US forests. *Ecosystems* 17: 765–777.
- Sack L, Cowan PD, Jaikumar N, Holbrook NM. 2003. The 'hydrology' of leaves: co-ordination of structure and function in temperate woody species. *Plant, Cell & Environment* 26: 1343–1356.
- Sack L, Melcher PJ, Liu WH, Middleton E, Pardee T. 2006. How strong is intracanalopy leaf plasticity in temperate deciduous trees? *American Journal of Botany* 93: 829–839.
- Sack L, Scoffoni C. 2013. Leaf venation: structure, function, development, evolution, ecology and applications in the past, present and future. *New Phytologist* 198: 983–1000.
- Salisbury EJ. 1928. On the causes and ecological significance of stomatal frequency, with special reference to the woodland flora. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 216: 1–65.
- Sanches MC, Ribeiro SP, Dalvi VC, Barbosa da Silva Junior M, Caldas de Sousa H, Pires de Lemos-Filho J. 2010. Differential leaf traits of a neotropical tree *Cariniana legalis* (Mart.) Kuntze (Lecythidaceae): comparing saplings and emergent trees. *Trees* 24: 79–88.
- Scafaro AP, Fan Y, Posch BC, Garcia A, Coast O, Atkin OK. 2021. Responses of leaf respiration to heatwaves. *Plant, Cell & Environment* 44: 2090–2101.
- Scartazza A, Di Baccio D, Bertolotto P, Gavrichkova O, Matteucci G. 2016. Investigating the European beech (*Fagus sylvatica* L.) leaf characteristics along the vertical canopy profile: leaf structure, photosynthetic capacity, light energy dissipation and photoprotection mechanisms. *Tree Physiology* 36: 1060–1076.
- Scharnweber T, Heinze L, Cruz-García R, van der Maaten-Theunissen M, Wilmking M. 2019. Confessions of solitary oaks: we grow fast but we fear the drought. *Dendrochronologia* 55: 43–49.
- Scheffers B, Edwards D, Diesmos A, Williams S, Evans T. 2013. Microhabitats reduce animal's exposure to climate extremes. *Global Change Biology* 20: 495–503.
- Schreuder MDJ, Brewer CA, Heine C. 2001. Modelled influences of non-exchanging trichomes on leaf boundary layers and gas exchange. *Journal of Theoretical Biology* 210: 23–32.
- Schymanski SJ, Or D, Zwieniecki M. 2013. Stomatal control and leaf thermal and hydraulic capacitances under rapid environmental fluctuations. *PLoS ONE* 8: e54231.
- Sellers PJ. 1985. Canopy reflectance, photosynthesis and transpiration. *International Journal of Remote Sensing* 6: 1335–1372.
- Sharkey TD. 2005. Effects of moderate heat stress on photosynthesis: importance of thylakoid reactions, rubisco deactivation, reactive oxygen species, and thermotolerance provided by isoprene. *Plant, Cell & Environment* 28: 269–277.

- Sharkey TD, Monson RK. 2014. The future of isoprene emission from leaves, canopies and landscapes. *Plant, Cell & Environment* 37: 1727–1740.
- Sharkey TD, Wiberley AE, Donohue AR. 2008. Isoprene emission from plants: why and how. *Annals of Botany* 101: 5–18.
- Shaw R. 1977. Secondary wind speed maxima inside plant canopies. *Journal of Applied Meteorology* 16: 514–521.
- Shugart HH, Wang B, Fischer R, Ma J, Fang J, Yan X, Huth A, Armstrong AH. 2018. Gap models and their individual-based relatives in the assessment of the consequences of global change. *Environmental Research Letters* 13: 033001.
- Sillett SC, Van Pelt R, Koch GW, Ambrose AR, Carroll AL, Antoine ME, Mifsud BM. 2010. Increasing wood production through old age in tall trees. *Forest Ecology and Management* 259: 976–994.
- Šimpraga M, Verbeeck H, Bloemen J, Vanhaecke L, Demarcke M, Joó E, Pokorska O, Amelynck C, Schoon N, Dewulf J *et al.* 2013. Vertical canopy gradient in photosynthesis and monoterpenoid emissions: an insight into the chemistry and physiology behind. *Atmospheric Environment* 80: 85–95.
- Sitch S, Smith B, Prentice IC, Arneth A, Bondeau A, Cramer W, Kaplan JO, Levis S, Lucht W, Sykes MT *et al.* 2003. Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. *Global Change Biology* 9: 161–185.
- Slot M, Cala D, Aranda J, Virgo A, Michaletz ST, Winter K. 2021a. Leaf heat tolerance of 147 tropical forest species varies with elevation and leaf functional traits, but not with phylogeny. *Plant, Cell & Environment* 44: 2414–2427.
- Slot M, Kitajima K. 2015. General patterns of acclimation of leaf respiration to elevated temperatures across biomes and plant types. *Oecologia* 177: 885–900.
- Slot M, Krause GH, Krause B, Hernández GG, Winter K. 2019. Photosynthetic heat tolerance of shade and sun leaves of three tropical tree species. *Photosynthesis Research* 141: 119–130.
- Slot M, Nardwattanawong T, Hernández GG, Bueno A, Riederer M, Winter K. 2021b. Large differences in leaf cuticle conductance and its temperature response among 24 tropical tree species from across a rainfall gradient. *New Phytologist* 232: 1618–1631.
- Slot M, Rifai SW, Winter K. 2021c. Photosynthetic plasticity of a tropical tree species, *Tabebuia rosea*, in response to elevated temperature and [CO₂]. *Plant, Cell & Environment* 44: 2347–2364.
- Slot M, Winter K. 2017. *In situ* temperature response of photosynthesis of 42 tree and liana species in the canopy of two Panamanian lowland tropical forests with contrasting rainfall regimes. *New Phytologist* 214: 1103–1117.
- Smith B, Prentice IC, Sykes MT. 2001. Representation of vegetation dynamics in the modelling of terrestrial ecosystems: comparing two contrasting approaches within European climate space. *Global Ecology and Biogeography* 10: 621–637.
- Smith MN, Stark SC, Taylor TC, Ferreira ML, de Oliveira E, Restrepo-Coupe N, Chen S, Woodcock T, dos Santos DB, Alves LF *et al.* 2019. Seasonal and drought-related changes in leaf area profiles depend on height and light environment in an Amazon forest. *New Phytologist* 222: 1284–1297.
- Smith MN, Taylor TC, van Haren J, Rosolem R, Restrepo-Coupe N, Adams J, Wu J, de Oliveira RC, da Silva R, de Araujo AC *et al.* 2020. Empirical evidence for resilience of tropical forest photosynthesis in a warmer world. *Nature Plants* 6: 1225–1230.
- Smith WK, Carter GA. 1988. Shoot structural effects on needle temperatures and photosynthesis in conifers. *American Journal of Botany* 75: 496–500.
- Song Q, Sun C, Deng Y, Bai H, Zhang Y, Yu H, Zhang J, Sha L, Zhou W, Liu Y. 2020. Tree surface temperature in a primary tropical rain forest. *Atmosphere* 11: 798.
- Stark SC, Breshears DD, Aragón S, Villegas JC, Law DJ, Smith MN, Minor DM, de Assis RL, de Almeida DRA, de Oliveira G *et al.* 2020. Reframing tropical savannization: linking changes in canopy structure to energy balance alterations that impact climate. *Ecosphere* 11: e03231.
- Stark SC, Leitold V, Wu JL, Hunter MO, de Castilho CV, Costa FRC, McMahon SM, Parker GG, Shimabukuro MT, Lefsky MA *et al.* 2012. Amazon forest carbon dynamics predicted by profiles of canopy leaf area and light environment. *Ecology Letters* 15: 1406–1414.
- Staudt K, Serafimovich A, Siebicke L, Pyles RD, Falge E. 2011. Vertical structure of evapotranspiration at a forest site (a case study). *Agricultural and Forest Meteorology* 151: 709–729.
- Stovall AEL, Shugart H, Yang X. 2019. Tree height explains mortality risk during an intense drought. *Nature Communications* 10: 4385.
- Suzuki N, Mittler R. 2006. Reactive oxygen species and temperature stresses: a delicate balance between signaling and destruction. *Physiologia Plantarum* 126: 45–51.
- Tan Z-H, Zeng J, Zhang Y-J, Slot M, Gamo M, Hirano T, Kosugi Y, da Rocha HR, Saleska SR, Goulden ML *et al.* 2017. Optimum air temperature for tropical forest photosynthesis: mechanisms involved and implications for climate warming. *Environmental Research Letters* 12: 054022.
- Tang H, Dubayah R. 2017. Light-driven growth in Amazon evergreen forests explained by seasonal variations of vertical canopy structure. *Proceedings of the National Academy of Sciences, USA* 114: 2640–2644.
- Taylor TC, McMahon SM, Smith MN, Boyle B, Vielle C, van Haren J, Simova I, Meir P, Ferreira LV, de Camargo PB *et al.* 2018. Isoprene emission structures tropical tree biogeography and community assembly responses to climate. *New Phytologist* 220: 435–446.
- Taylor TC, Smith MN, Slot M, Feeley KJ. 2019. The capacity to emit isoprene differentiates the photosynthetic temperature responses of tropical plant species. *Plant, Cell & Environment* 42: 2448–2457.
- Taylor TC, Wisniewski WT, Alves EG, de Oliveira RC, Saleska SR. 2021. A new field instrument for leaf volatiles reveals an unexpected vertical profile of isoprenoid emission capacities in a tropical forest. *Frontiers in Forests and Global Change* 74: doi: 10.3389/ffgc.2021.668228.
- Tepley AJ, Thompson JR, Epstein HE, Anderson-Teixeira KJ. 2017. Vulnerability to forest loss through altered postfire recovery dynamics in a warming climate in the Klamath Mountains. *Global Change Biology* 23: 4117–4132.
- Teskey R, Werten T, Bauweraerts I, Amey M, McGuire MA, Steppe K. 2015. Responses of tree species to heat waves and extreme heat events. *Plant, Cell & Environment* 38: 1699–1712.
- Thomas SC, Winner WE. 2002. Photosynthetic differences between saplings and adult trees: an integration of field results by meta-analysis. *Tree Physiology* 22: 117–127.
- Tibbitts TW. 1979. Humidity and plants. *BioScience* 29: 358–363.
- Tiwari R, Gloor E, da Cruz WJA, Marimon BS, Marimon-Junior BH, Reis SM, de Souza IA, Krause HG, Slot M, Winter K *et al.* 2021. Photosynthetic quantum efficiency in south-eastern Amazonian trees may be already affected by climate change. *Plant, Cell & Environment* 44: 2428–2439.
- Trouillier M, van der Maaten-Theunissen M, Scharnweber T, Würth D, Burger A, Schnittler M, Wilmking M. 2018. Size matters – a comparison of three methods to assess age- and size-dependent climate sensitivity of trees. *Trees* 33: 183–192.
- Turnbull MH, Whitehead D, Tissue DT, Schuster WSF, Brown KJ, Griffin KL. 2003. Scaling foliar respiration in two contrasting forest canopies. *Functional Ecology* 17: 101–114.
- Tymen B, Vincent G, Courtois EA, Heurtebize J, Dauzat J, Marechaux I, Chave J. 2017. Quantifying micro-environmental variation in tropical rainforest understory at landscape scale by combining airborne LiDAR scanning and a sensor network. *Annals of Forest Science* 74: 32.
- Urban J, Ingwers M, McGuire MA, Teskey RO. 2017. Stomatal conductance increases with rising temperature. *Plant Signaling & Behavior* 12: e1356534.
- Urban O, Kosvancová M, Marek MV, Lichtenthaler HK. 2007. Induction of photosynthesis and importance of limitations during the induction phase in sun and shade leaves of five ecologically contrasting tree species from the temperate zone. *Tree Physiology* 27: 1207–1215.
- Van Wittenberghe S, Adriaenssens S, Staelens J, Verheyen K, Samson R. 2012. Variability of stomatal conductance, leaf anatomy, and seasonal leaf wettability of young and adult European beech leaves along a vertical canopy gradient. *Trees* 26: 1427–1438.
- Vårhammar A, Wallin G, McLean CM, Dusenke ME, Medlyn BE, Hasper TB, Nsabimana D, Uddling J. 2015. Photosynthetic temperature responses of tree species in Rwanda: evidence of pronounced negative effects of high temperature in montane rainforest climax species. *New Phytologist* 206: 1000–1012.
- Vickers CE, Gershenson J, Lerdau MT, Loreto F. 2009. A unified mechanism of action for volatile isoprenoids in plant abiotic stress. *Nature Chemical Biology* 5: 283–291.
- Vogel S. 1968. “Sun leaves” and “shade leaves”: differences in convective heat dissipation. *Ecology* 49: 1203–1204.
- Vogel S. 2009. Leaves in the lowest and highest winds: temperature, force and shape. *New Phytologist* 183: 13–26.

- Wang B, Chen T, Li C, Xu G, Wu G, Liu G. 2022. Discrepancy in growth resilience to drought among different stand-aged forests declines going from a semi-humid region to an arid region. *Forest Ecology and Management* 511: 120135.
- Way DA. 2019. Just the right temperature. *Nature Ecology & Evolution* 3: 718–719.
- Way DA, Pearcy RW. 2012. Sunflecks in trees and forests: from photosynthetic physiology to global change biology. *Tree Physiology* 32: 1066–1081.
- Webster C, Westoby M, Rutter N, Jonas T. 2018. Three-dimensional thermal characterization of forest canopies using UAV photogrammetry. *Remote Sensing of Environment* 209: 835–847.
- Weerasinghe LK, Creek D, Crous KY, Xiang S, Liddell MJ, Turnbull MH, Atkin OK. 2014. Canopy position affects the relationships between leaf respiration and associated traits in a tropical rainforest in Far North Queensland. *Tree Physiology* 34: 564–584.
- van de Weg MJ, Meir P, Grace J, Ramos GD. 2012. Photosynthetic parameters, dark respiration and leaf traits in the canopy of a Peruvian tropical montane cloud forest. *Oecologia* 168: 23–34.
- Wong SC, Cowan IR, Farquhar GD. 1979. Stomatal conductance correlates with photosynthetic capacity. *Nature* 282: 424–426.
- Woodward FI, Lomas MR. 2004. Vegetation dynamics – simulating responses to climatic change. *Biological Reviews* 79: 643–670.
- Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JHC, Diemer M *et al.* 2004. The worldwide leaf economics spectrum. *Nature* 428: 821–827.
- Wu J, Albert LP, Lopes AP, Restrepo-Coupe N, Hayek M, Wiedemann KT, Guan K, Stark SC, Christoffersen B, Prohaska N *et al.* 2016. Leaf development and demography explain photosynthetic seasonality in Amazon evergreen forests. *Science* 351: 972–976.
- Wyka TP, Oleksyn J, Zytowski R, Karolewski P, Jagodziński AM, Reich PB. 2012. Responses of leaf structure and photosynthetic properties to intra-canopy light gradients: a common garden test with four broadleaf deciduous angiosperm and seven evergreen conifer tree species. *Oecologia* 170: 11–24.
- Wylie RB. 1951. Principles of foliar organization shown by sun-shade leaves from ten species of deciduous dicotyledonous trees. *American Journal of Botany* 38: 355–361.
- Xu B, Arain MA, Black TA, Law BE, Pastorello GZ, Chu H. 2020. Seasonal variability of forest sensitivity to heat and drought stresses: a synthesis based on carbon fluxes from North American forest ecosystems. *Global Change Biology* 26: 901–918.
- Xu C-Y, Griffin KL. 2006. Seasonal variation in the temperature response of leaf respiration in *Quercus rubra*: foliage respiration and leaf properties. *Functional Ecology* 20: 778–789.
- Yang PC, Black TA, Neumann HH, Novak MD, Blanken PD. 1999. Spatial and temporal variability of CO₂ concentration and flux in a boreal aspen forest. *Journal of Geophysical Research: Atmospheres* 104: 27653–27661.
- Yoder BJ, Ryan MG, Waring RH, Schoettle AW, Kaufmann MR. 1994. Evidence of reduced photosynthetic rates in old trees. *Forest Science* 40: 513–527.
- Zellweger F, Coomes D, Lenoir J, Depauw L, Maes SL, Wulf M, Kirby KJ, Brunet J, Kopecký M, Máliš F *et al.* 2019. Seasonal drivers of understorey temperature buffering in temperate deciduous forests across Europe. *Global Ecology and Biogeography* 28: 1774–1786.
- Zellweger F, De Frenne P, Lenoir J, Vangansbeke P, Verheyen K, Bernhardt-Römermann M, Baeten L, Hédél R, Berki I, Brunet J *et al.* 2020. Forest microclimate dynamics drive plant responses to warming. *Science* 368: 772–775.
- Zhang J-L, Poorter L, Hao G-Y, Cao K-F. 2012. Photosynthetic thermotolerance of woody savanna species in China is correlated with leaf life span. *Annals of Botany* 110: 1027–1033.
- Zhou H, Xu M, Pan H, Yu X. 2015. Leaf-age effects on temperature responses of photosynthesis and respiration of an alpine oak, *Quercus aquifolioides*, in southwestern China. *Tree Physiology* 35: 1236–1248.
- Zweifel R, Bohm JP, Hasler R. 2002. Midday stomatal closure in Norway spruce – reactions in the upper and lower crown. *Tree Physiology* 22: 1125–1136.
- Zwieniecki MA, Boyce CK, Holbrook NM. 2004. Hydraulic limitations imposed by crown placement determine final size and shape of *Quercus rubra* L. leaves. *Plant, Cell & Environment* 27: 357–365.

Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Vertical gradients in micrometeorological conditions for all forested sites in the National Ecological Observatory Network.

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.

Notes S1 Biophysical drivers of T_{leaf} .

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

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