Review

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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 (CO_2) 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').

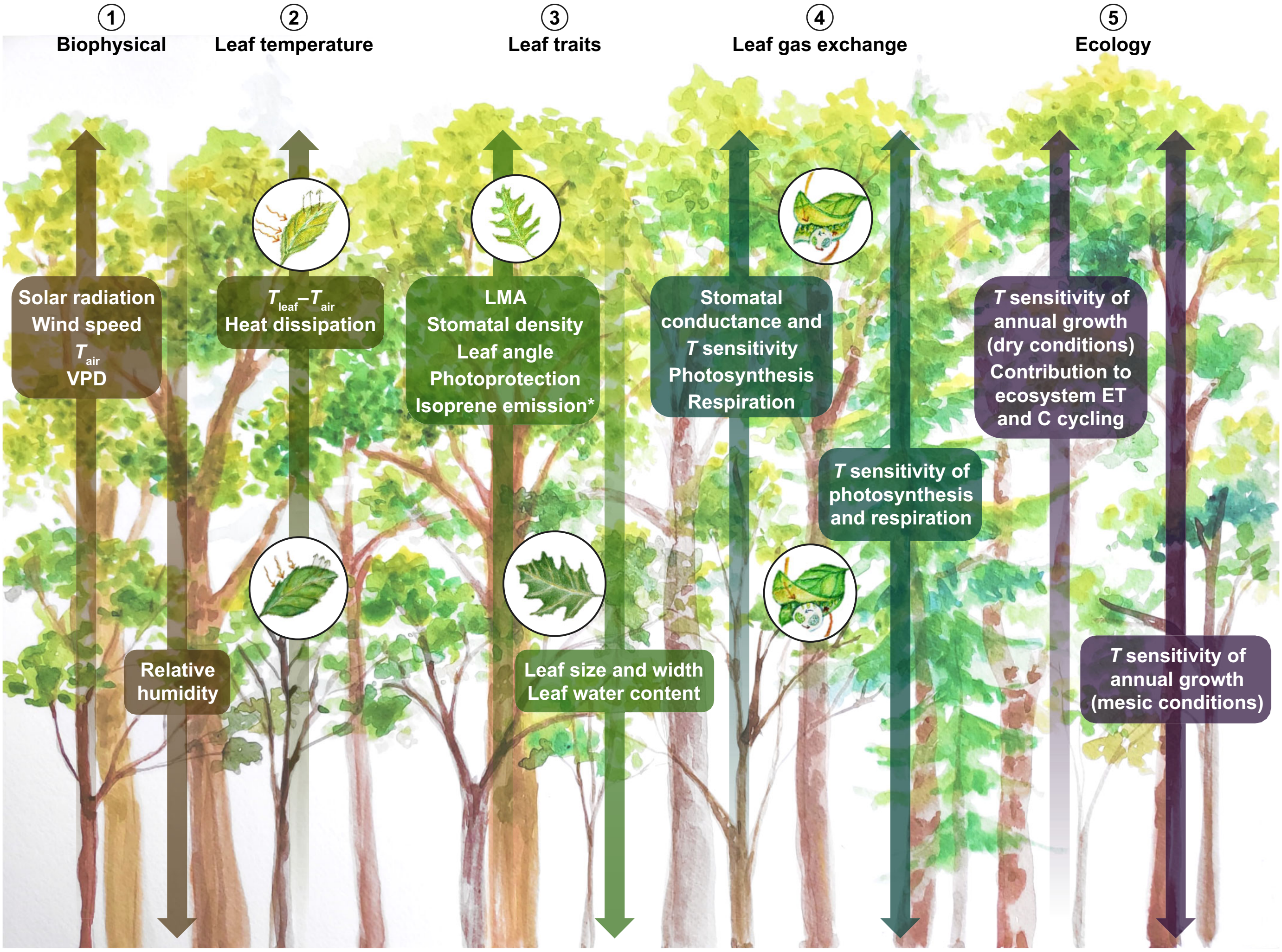


Fig. 1 Schematic summarizing typical vertical gradients in (1) biophysical environment, (2) leaf temperature (T_{leaf}), (3) leaf traits, (4) leaf gas exchange, and (5) tree and ecosystem ecology within closed-canopy forests during daytime growing season conditions. Arrows indicate direction of increase, 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; $T_{leaf} - T_{air}$, 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

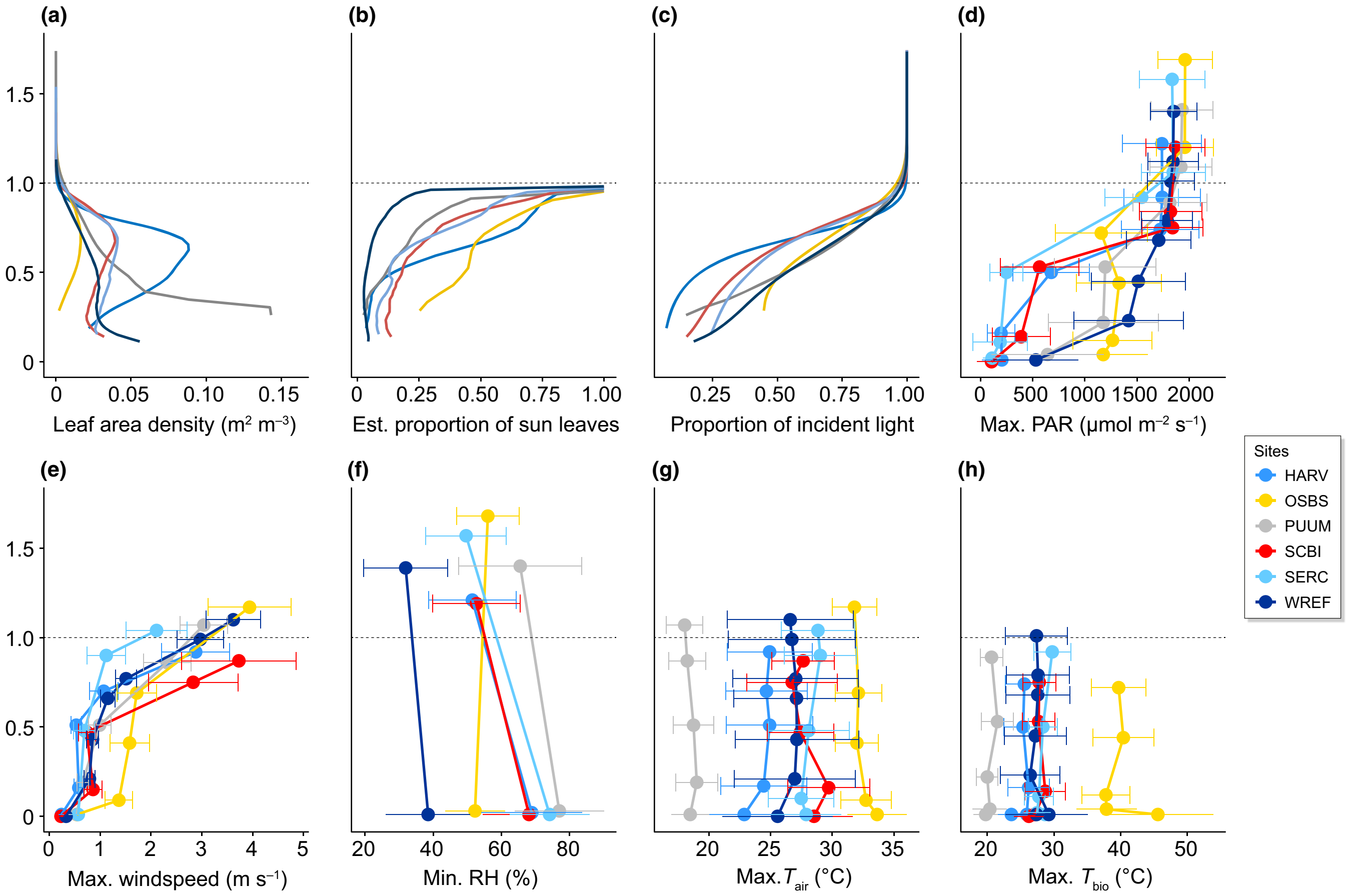


Fig. 2 Vertical gradients in the biophysical environment for six USA forest sites in the National Ecological Observatory Network (NEON). Height profiles, normalized relative to the top of the canopy, are shown for: growing season (a) modeled leaf area density, (b) estimated proportion of sun leaves, and (c) proportion of light incident to the top of the canopy (as fraction relative to top of canopy), and for July mean ± 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 CO_2 and water vapor Atmospheric CO_2 concentrations tend to be higher near the ground at night, associated with plant and soil respiration, but the elevated CO_2 quickly dissipates during the day such that CO_2 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 CO_2 concentrations near the ground during some parts of the day (e.g. 6% of C fixation from recently respired CO_2; Brooks *et al.*, 1997), gradients in CO_2 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_b 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

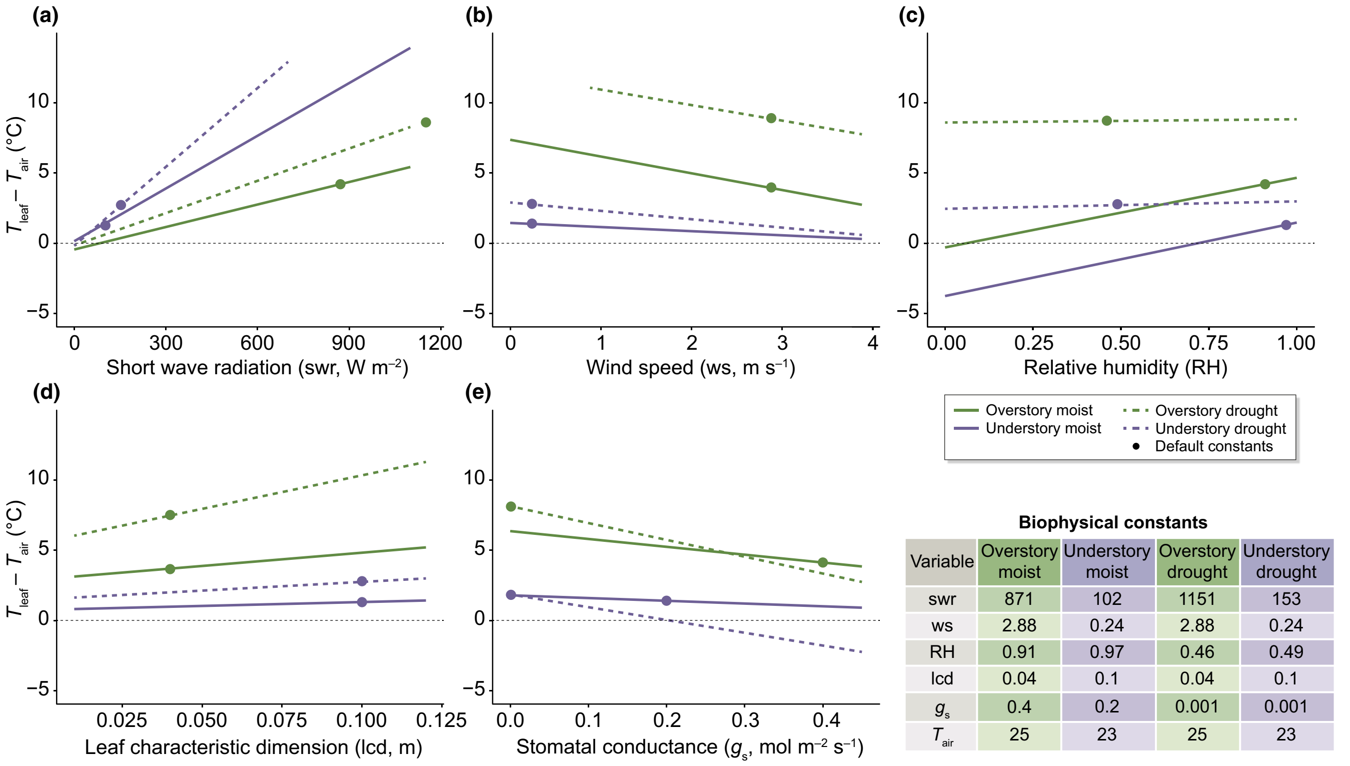
T_{leaf} is strongly tied to, and usually within a few degrees of, T_{air} (Rey-Sánchez *et al.*, 2016; Drake *et al.*, 2020) but can be substantially warmer or cooler under certain conditions (Notes S1; Doughty & Goulden, 2008; Vogel, 2009; Rey-Sánchez *et al.*, 2016). Deviation of T_{leaf} from T_{air} 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 $T_{leaf} - T_{air}$ and thus are often warmer than understory leaves (Fig. 3a). However, higher wind speeds reduce $T_{leaf} - T_{air}$ (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°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, $T_{leaf} - T_{air}$ 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; Fauset *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 $T_{leaf} - T_{air}$ (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 $T_{leaf} - T_{air}$ 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 $T_{leaf} - T_{air}$ 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 *c.* 5°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



Biophysical constants

Variable	Overstory moist	Understory moist	Overstory drought	Understory drought
swr	871	102	1151	153
ws	2.88	0.24	2.88	0.24
RH	0.91	0.97	0.46	0.49
lcd	0.04	0.1	0.04	0.1
g_s	0.4	0.2	0.001	0.001
T_{air}	25	23	25	23

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_b 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_b). Steeper leaf angles reduce midday radiation loads and thereby decreasing $T_{\mathrm{leaf}} - T_{\mathrm{air}}$ (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_b; 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 $\delta^{13}C$ (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	TrB, TeB, BoN	7, 8, 10
			↓ L	TrB, TeB, BoN	7, 8, 3, 10
Leaf mass per area (or inverse of specific leaf area)	LMA (or 1/SLA)	$g\ cm^{-2}$	↑ H	TrB, TeB, TeN, BoN	1, 55, 64, 7, 2, 3, 4, 6
			↑ L	TrB, TeB, TeN, BoN	1, 7, 2, 3, 5, 6
Leaf thickness		μm	↑ H	TrB, TeB, TeN	15, 11, 2, 13, 16
			↑ L	TrB, TeB, TeN	11, 15, 2, 5
Leaf density		$g\ cm^{-3}$	↑ H	TeB	2
			↑ L	TrB, TeB	6, 2
			≈ L	TeN	5
Pinnate lobation		cm^2	↑ H	TeB	3
			↓ H	TeB	8
			↑ L	TeB	8, 3
Leaf packing		$n\ cm^{-1}$ stem	↑ L	TeN	25, 26
Blade inclination angle (vertical)	φB	°	↑ H	TrB, TeB	21, 22, 23
			↑ L	TrB, TeB	21, 24, 23, 22, 48
Trichome density		mm^{-2}	↑ H	TrB	17
			↑ L	TrB, TeB	17, 18, 19, 20
Stomatal density	$D_{stomata}$	mm^{-2}	↑ H	TrB, TeB, TeN	11, 12, 3, 13, 4
			↑ L	TrB, TeB	12, 11, 3
Total vein density	VLA	$mm\ mm^{-2}$	↑ H	TeB	46
			↑ L	TeB	46, 47
Minor vein density	VLA_{min}	$mm\ mm^{-2}$	↑ H	TeB	14
			↑ L	TeB	14, 47
Upper cuticle thickness	CT	μm	↑ H	TrB, TeN	27, 4
			↑ L	TrB, TeB	27, 28
Leaf optical properties					
PAR absorptance		%	≈ ↑ H	TrB	42, 45
			≈ ↑ L	TrB	42, 45
Absorptance efficiency per unit biomass		$\%\ g^{-1}$	↓ H	TrB	42, 45
			↓ L	TrB	42, 45
PAR transmittance		%	↓ H	TrB	42, 45
			↓ L	TrB	42, 45
Reflectance		%	≈ H	TrB	42, 45
			↑ H	BoN	6
			≈ L	TrB	42, 45
Traits related to metabolic capacity and efficiency					
Nitrogen content	N	$g\ m^{-2}$	↑ H	TrB, TeB, TeN, BoN	55, 64, 7, 29, 30, 32, 31, 9
		$mg\ g^{-1}$	≈ ↓ H	TrB, TeB, TeN	55, 15, 7, 29, 30, 32, 34
			≈ ↓ L	TrB, TeB, TeN	7, 35, 29, 30, 32, 5
Phosphorus content	P	$g\ m^{-2}$	↑ H	TrB, TeB, TeN	55, 15, 36, 1, 37
			↑ L	TrB, TeB, TeN	15, 5
			≈ L	TrB, TeB	1
		$mg\ g^{-1}$	≈ ↓ H	TrB	55, 15, 35, 1
			≈ L	TrB, TeB	15, 35, 1
Chlorophyll content	Chl	$mg\ cm^{-2}$	↓ H	TrB, TeB	40, 41
			↓ L	TrB, TeB	42, 41
Chlorophyll *a*/*b* ratio	chl*a*/*b*	$mol\ mol^{-1}$	↑ H	TrB, TeB, BoN	42, 30, 6
			↑ L	TrB, TeB, BoN	42, 30, 39, 22, 6
Carbon isotope ratio	$\delta^{13}C$	‰	↑ H	TrB, TeB, TeN	55, 64, 7, 43, 31
			↑ L	TrB, TeB, TeN	7, 29, 31
Intercellular CO_2 concentration	C_i	$\mu mol\ mol^{-1}$	↓ H	TeB, BoN	51, 30, 44
			↓ L	TeB	30, 44
Biochemical protection against light and heat damage					
β-Carotene and lutein		$\mu mol\ m^{-2}$	↑ H	TrB, TeB, BoN	30, 42, 6
			↑ L	TrB, TeB, BoN	30, 38, 6
Xanthophyll cycle pigments	VAZ	$\mu mol\ m^{-2}$	↑ H	TrB, TeB	38, 30, 22
			↑ L	TrB, TeB	39, 30
Abundance isoprene emitters		%	↑ H (peak in mid-canopy)	TrB	49
			↑ L	TeB	50

Table 1 (Continued)

Trait	Symbol	Units	Response[1]	Forest type(s)[2]	Reference(s)[3]
Isoprene emission rate	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	T_{50}	°C	↓ H[4]	TrS	52
			≈ ↑ L	TrB, TeB	53, 54
Critical temperature beyond which F_v/F_m declines	T_{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.

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

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

[3] 1. 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. Marenco *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).

[4] Composite 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 (Laothawornkitkul *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 bothy 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	mmol m^{-2} s^{-1}	↑ H	TrB	3
		mm s^{-1}	↑ H	TeN	12
			≈ L	TeN	12
Leaf hydraulic conductance	K_{leaf}	m^{-2} s^{-1} MPa^{-1}	↑ L	TeB	
Cuticle conductance	g_{min}	mmol m^{-2} s^{-1}	↑ L	TrB	38
Max stomatal conductance	$g_{s\ max}$	mol m^{-2} s^{-1}	↑ H	TrB, TeB, BoN	1, 2, 4
			↑ L	TrB, TeB, TeN, BoN	8, 9, 10, 7, 4
Stomatal conductance limitation	g_s	mol m^{-2} s^{-1}	↑ H	TrB, TeN	9, 39, 5, 6, 7
			↑ L	TrB, TeN	9, 39, 7, 27
Stomatal conductance at optimal temperature	g_s at T_{opt}	mol m^{-2} s^{-1}	≈↑ H	TeB	11
			↓ H	TrB	39
			≈↑ L	TrB	8
Photosynthesis					
Maximum photosynthetic capacity	A_{max}	mol m^{-2} s^{-1}	↑ H	TrB, TeB, BoN	14, 11, 15, 4
			≈↓ H	TeB	16
			↑ L	TrB, TeB, TeN, BoN	14, 17, 18, 19, 10, 4
		nmol g^{-1} s^{-1}	≈ H	TrB	20, 2
			≈ L	TrB, TeB, TeN	20, 19
Maximum light-saturated net photosynthesis	A_{sat}	µmol m^{-2} s^{-1}	↑ H	TrB, TeB	21, 22
			↑ L	TrB, TeB	8, 22
A_{sat} at optimum temperature	A_{opt}	µmol m^{-2} s^{-1}	≈↑ H	TrB, TeB	13, 11
			↑ H	TrB	39
			↑ L	TrB	8, 13
Optimum temperature for photosynthesis	T_{opt}	°C	≈ H	TrB, TeB	23, 11, 13
			↓ H	TrB	39
			≈ L	TrB, TeB	9, 8, 11
Photosynthetic light compensation point	LCP	µmol m^{-2}	↑ H	TrB, TeB, TeN	24, 16
			↑ L	TrB, TeB, TeN	8, 17, 16
Maximal carboxylation rate	V_{cmax}	µmol m^{-2} s^{-1}	↑ H	TrB, TeB	2,39, 22, 14
			↑ L	TrB, TeB, BoN	9, 39, 22, 14, 10
		nmol g^{-1} s^{-1}	≈ H	TrB, TeB	2, 2
			≈ L	TrB, TeB	2, 22
		nmol CO_2 g^{-1} s^{-1}	≈↓ L	TeB	25
Optimum temperature for V_{cmax}	V_{cmax} (T_{opt})	µmol m^{-2} s^{-1}	≈↑ H	TeB	11
			≈ L	TrB	9
Electron transport rate	J_{max}	µmol m^{-2} s^{-1}	↑ H	TrB, TeB	2, 39, 36, 22, 14
			↑ L	TrB, TeB	9, 39, 22, 26, 14
		nmol g^{-1} s^{-1}	≈ H	TrB, TeB	2, 22
			≈ L	TrB, TeB	2, 22
		nmol e^{-1} g^{-1} s^{-1}	≈↓ L	TeB	25
Optimal temperature of J_{max}	T_{optETR}	°C	↓ H	TrB	39
	J_{max} (T_{opt})	µmol m^{-2} s^{-1}	≈ 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	µmol CO_2 m^{-2} s^{-1}	↑ H	TrB, TeB, TeN	36, 28, 29, 30
		µmol CO_2 kg^{-1} s^{-1}	≈ H	TrB, TeB, TeN	28, 29
			↑ L	TrB, TeN	28, 30
Light respiration	R_L	µmol m^{-2} s^{-1}	↑ H	TrB	21
			↑ L	TrB	21
Dark respiration	R_{dark}	µmol m^{-2} s^{-1}	↑ H	TrB, TeB, BoN	21, 14, 31, 22, 38
			↑ L	TrB, TeB, TeN, BoN	21, 14, 22, 17, 10, 35
		nmol g^{-1} s^{-1}	≈↑ H	TrB	2, 32
			≈ L	TrB	2, 32
R_{dark} at reference T	R_{dark} at reference T	µmol m^{-2} s^{-1}	↑ H	TrB, TeB, TeN	21, 14, 31, 29
		µmol (kg leaf)$^{-1}$ s^{-1}	↑ H	TrB, TeB, TeN	21, 14, 31, 21
		µmol (kg N)$^{-1}$ s^{-1}	↑ H	TeB, TeN	3, 29
		µmol m^{-2} s^{-1}	↑ 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}	°C^{-1}	≈ H	TrB, TeB, TeN	21, 36, 31, 30
		°C^{-1}	≈ ↑ H	TeB, TeN	3, 29
			≈ ↓ L	TrB, TeB, TeN	21, 31, 30
			↑ L	TeB	33
Activation energy of R_{dark}	E_0	kJ mol^{-1} K^{-1}	≈ H	TrB, TeB, TeN	21, 34, 29
			≈ L	TrB	21, 8

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

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

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

[3] 1. Kafuti *et al*. (2020); 2. Van Wittenberghe *et al*. (2012); 3. Roberts *et al*. (1990); 4. Dang *et al*. (1997); 5. Marenco *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_{cmax}) 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 ≥ 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; Piponiot *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.

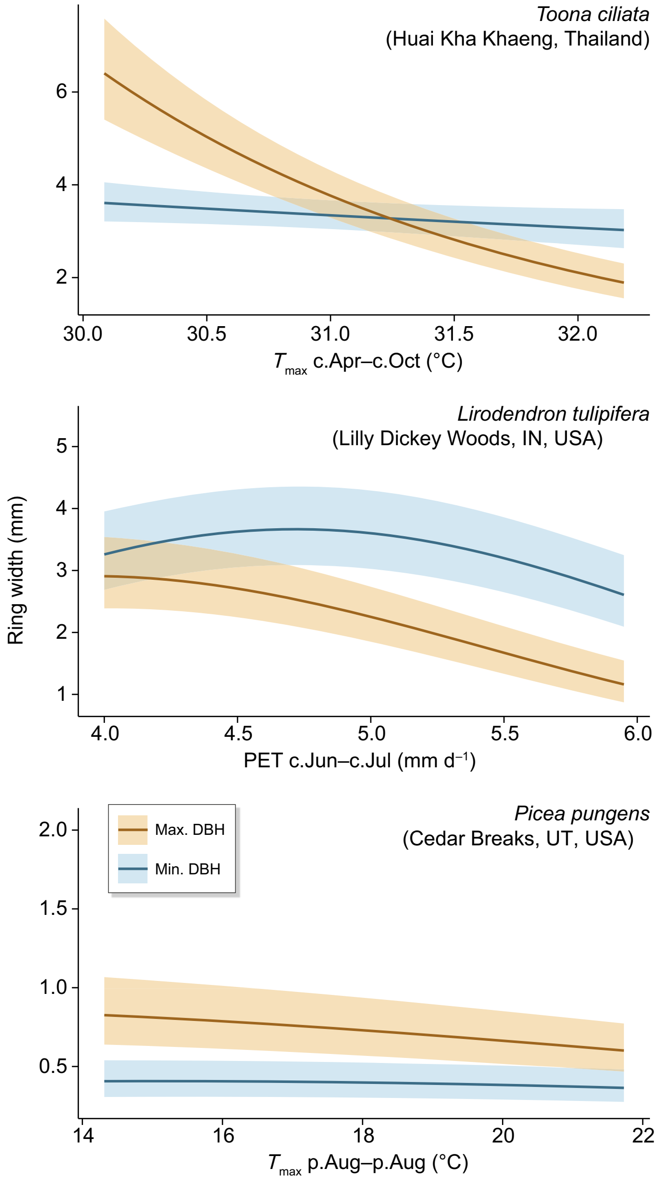


Fig. 4 Examples of tree ring evidence for greater interannual temperature sensitivity of annual growth for large than for small trees. Across three sites and species, trees with large diameter at breast height (DBH) had more negative growth responses to high maximum temperature (T_{max}) or potential 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

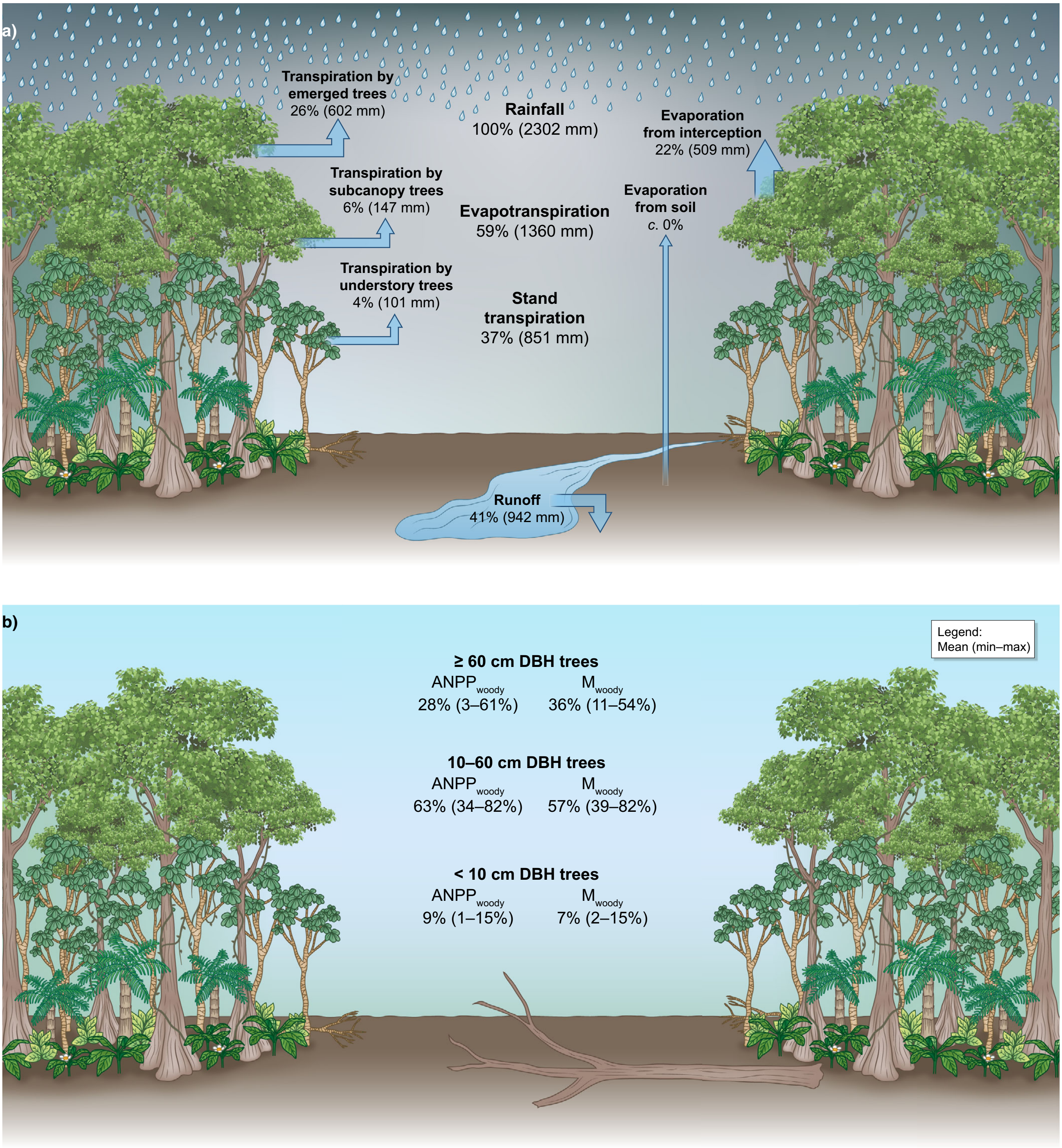


Fig. 5 Vertical partitioning of (a) evapotranspiration and (b) carbon fluxes in tropical forests. Panel (a) is from Kunert *et al*. (2017); (b) presents averages for 14 tropical forests from Piponiot *et al*. (2022). DBH, diameter at breast height; ANPP, aboveground net primary productivity; M_{woody},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

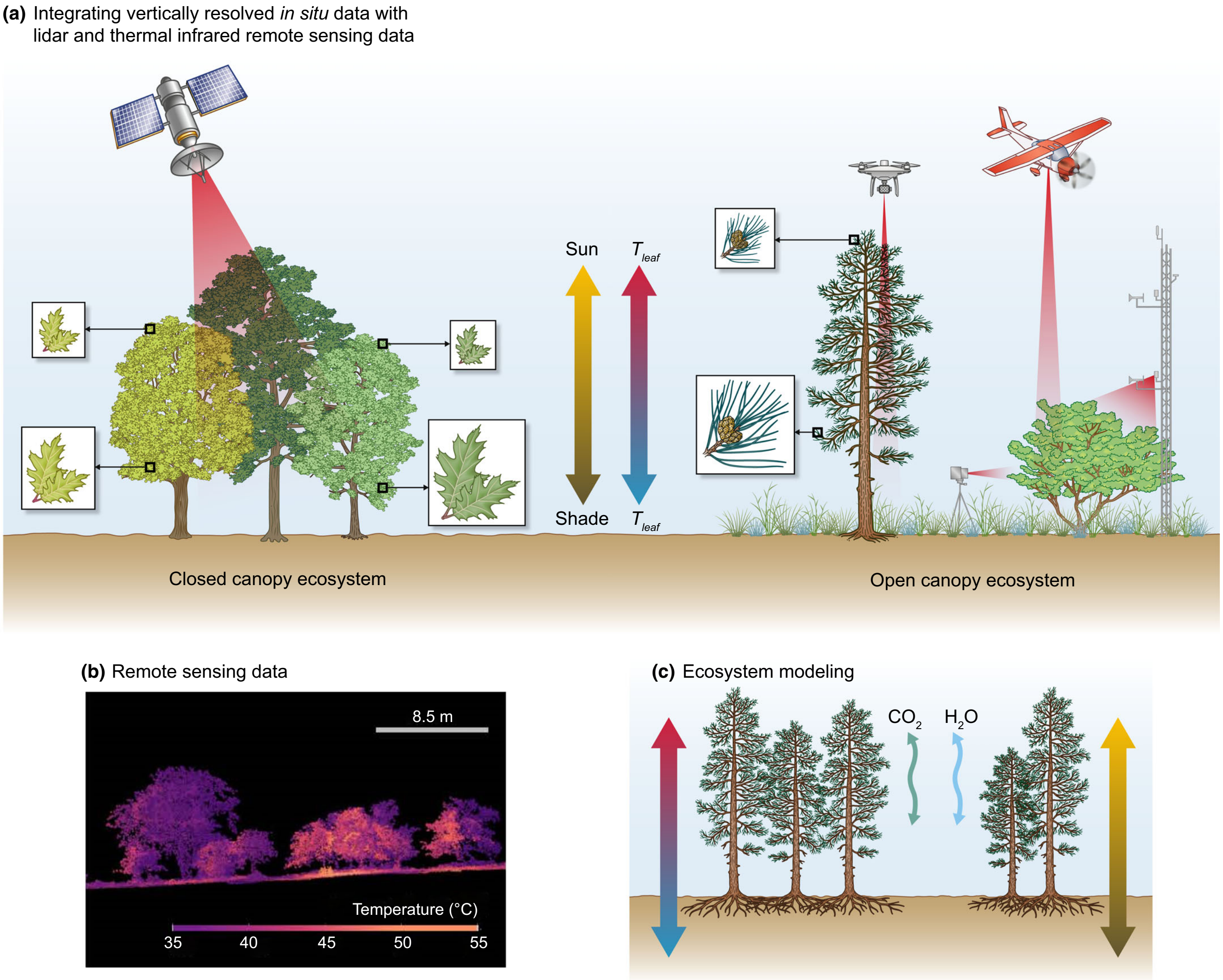


Fig. 6 LiDAR and thermal remote sensing data can be used to measure vertical forest structure and plant thermal signatures at increasingly large scales. (a, b) Integrating *in situ* and remote sensing measurements will support our ability to scale understanding of vertical gradients within and across 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 a increasing interest in confronting models directly with field measurements (Fisher & Koven, 2020; Maclean & Klinges, 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 accuratly 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. Ensuant 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).

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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.